

Reproduction and Early Development of the Paddlefish

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ABSTRACT

Paddlefish, *Polyodon spathula* (Walbaum), were observed spawning over gravel bars in the Osage River, Missouri. Eggs and prolarvae were collected. Eggs were hatched and young paddlefish were reared. The external features of the egg and prolarvae, hatching, and early behavior of the larvae are described. The effect of impoundment of rivers on the paddlefish population is discussed.

INTRODUCTION

In recent years a snagging fishery for paddlefish, *Polyodon spathula* (Walbaum), has become very important in the headwaters of the Lake of the Ozarks in the vicinity of Warrenton, Missouri, and in its major tributary, the Osage River, for 55 miles upstream to Osceola, Missouri. Annual harvests of 100 tons or more of fish which weighed an average of 50 pounds have been made during the spawning season, March 15 to May 15. In a study of this fishery and the life history of the paddlefish, the first observations of spawning and reproduction ever recorded for this species were made, and details of hatching and development are available for the first time.

The paddlefish has been the subject of many studies. At the 1910 meeting of the American Fisheries Society Dr. B. W. Evermann, commenting after a report on the paddlefish (Hussakof, 1911) said, "The queerest thing about the paddlefish is this, that no one has been able to locate definitely its spawning grounds and to find the young fry. . . . That is one of the most important and interesting problems to be undertaken. It has been attempted by several embryologists and others, but it is, to work out the life history of the paddlefish on a spoonbill." Subsequent exhaustive researches have never revealed definite evidence of spawning, egg deposition and development, or newly hatched larvae, until the time of this

study. The two smallest paddlefish previously reported were both 17 millimeters long. The first was collected in 1932 by Dr. David H. Thompson (1933) in a collection of seven which were from 17 to 20 millimeters long. These were collected from the Mississippi River near Grand Tower, Illinois. Dr. Thompson and Mr. P. G. Barnickol collected four small paddlefish 17 to 26 millimeters long, also from the Mississippi River near Cape Girardeau, Missouri, on May 29, 1944 (Larimore, 1949).

SPAWNING POPULATION

Netting studies indicated that some paddlefish were present in the headwaters of the Lake of the Ozarks in late February. As the water warmed, more appeared. Extensive upstream migration, however, did not take place until the water had warmed to near 50°F., and there was a rise of several feet in the water level of the Osage River. Early in the season a rise of several days' duration was required for the fish to move all the way to Osceola, where a dam 14 feet high blocks further migration. Later in the season they arrived at Osceola after only 2 or 3 days of high water.

Forty male paddlefish taken from the spawning population in 1959 averaged 55 inches long and 28.5 pounds in weight. They ranged from 47.5 to 65.5 inches in length and from 15 to 45 pounds in weight. Forty

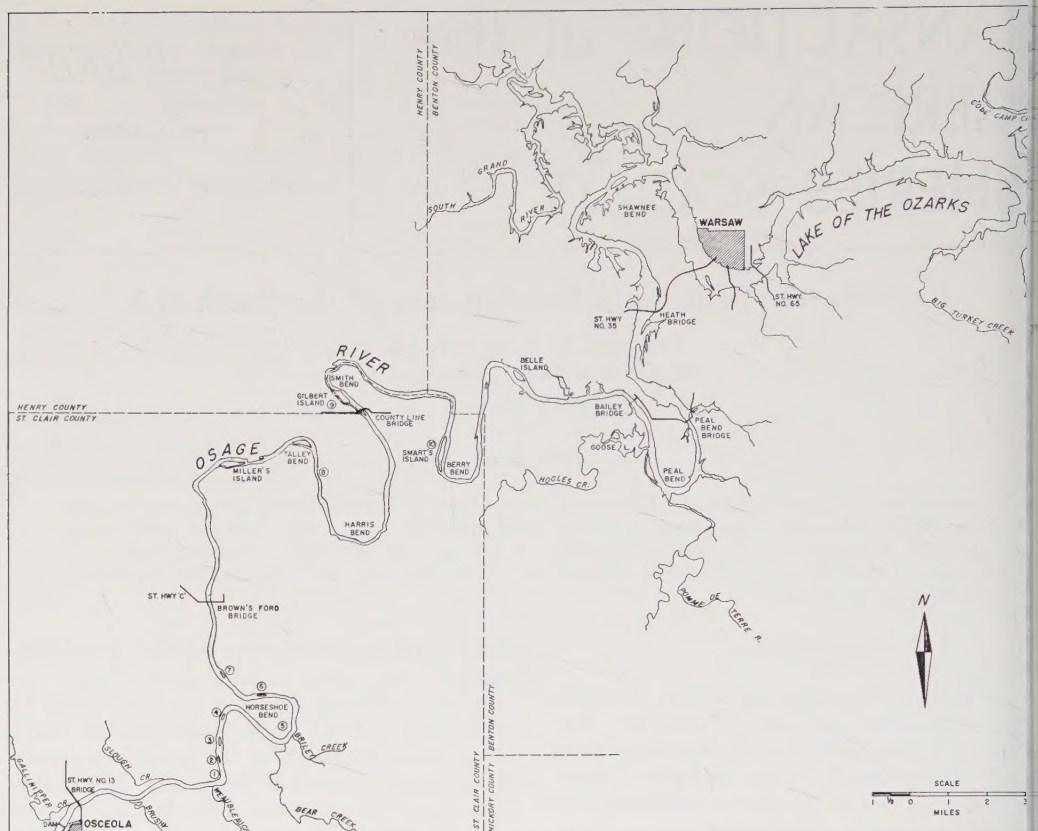


FIGURE 1.—Osage River and upper Lake of the Ozarks. Numbers indicate areas where paddlefish spawning was known to take place in 1960.

females were larger, averaging 60 inches long and 41.4 pounds in weight, with a range from 51.25 to 65.5 inches and from 24 to 57 pounds. Much of the greater weight of the females was due to the weight of the ovaries. These weighed 6 to 8 pounds in most ripe females.

On April 12, 1958, several ripe male and female paddlefish and one spent female were taken by fishermen in the Horseshoe Bend area of the Osage River (Figure 1). Immediately prior to this time the water level had been 9 feet above normal and was falling. Water temperature was 52°F. One female from which eggs were running and one ripe male were obtained at the same place from a fisherman. A half pint of these eggs was fertilized and kept alive a few days in aerated water. Another attempt at artificial hatching was made in April 1960, when eggs collected in the same manner were taken to a hatchery. These fungused and died in 3 days.

In 1959 no fully ripe or spawned-out male paddlefish were found. This was a year of few spring rises in water level. Rises that did occur were never over 5 feet and subsided quickly. Thus the majority of the fish did not have time to swim to the upstream spawning sites. It is not known whether they failed to spawn or chose downstream locations.

SPAWNING

Spawning of paddlefish first was observed during the late afternoon and evening of April 20, 1960, the seventh day after a 9-foot rise. Spawning occurred over a large gravel bar in the Osage River in rapidly flowing water opposite the mouth of Weaubleau Creek in St. Clair County, T.38 N., R.25 W., S.36 E. (number 1 on Figure 1). Most of the gravel varied from 1/2 inch to about 1 1/2 inches in diameter. In this area the Osage River is about 270 feet wide. Depths fluctuated considerably with the water level. At normal

els pools were 15 to 20 feet deep. Turbid-
was about 180 p.p.m. during the spawning
iod. The water temperature was 61°F.
st of the spawning activity occurred under-
er. The only indication on the surface was
appearance of single fish which, while
visible at the surface, would agitate the
caudal fin several times, then disappear after
few seconds. This occurred every few min-
throughout the late afternoon and
ning.

he sudden appearance of the fish and the
ef surface activity caused me to conclude
t the female was underwater with males,
that a spawning "rush" occurred from a
siderable distance under the surface dur-
which the eggs were released by a rapid
ation of the caudal of the female. Pre-
ably, accompanying males then released
t. The surfacing appeared to be the end
the spawning "rush" of the female. After
k the sound of the agitation of the caudal
the only evidence of spawning. Similar
ivity was seen on April 22 at the same loca-
a, but less frequently.

EGGS AND PROLARVAE

Verification that the behavior just de-
bed was spawning activity came on April
following a rapid fall in water level of
ut 7 feet. As soon as the gravel bar was
osed, paddlefish eggs and newly hatched
rae were found in the area where the
rent would have carried them from the
wning fish (Figure 2).

Eggs taken from snagged females, when
eased, were non-adhesive. Immediately
er fertilization a coating formed which
sed the egg to adhere to the first object it
ched. Most eggs had adhered singly to a
ble or rock. Adhesion was so strong that
he eggs were broken in attempts to remove
m. Dredging downstream from the gravel
s indicated that many eggs are swept
nstream and coated with debris before
oming attached. Some also were found on
er-logged twigs. The most favorable loca-
for hatching obviously was the clean-
pt gravel bar. Here they were not subject
iltation, and aeration was good.

The hatching larva also depended on the
vel and current. Some larvae were ob-
red on the gravel bars; other eggs from
gravel bars were hatched in aerated
aria. Paddlefish eggs hatch rather quickly,
arently in 7 days or less at temperatures
65° to 70°F. This was the longest time



FIGURE 2.—Closeup view of the gravel bar directly across the river from the mouth of Weaubleau Creek. Paddlefish spawning was observed to take place in the water over the gravel in the right foreground. Eggs and prolarvae were collected first from the gravel in the left rear.

taken to hatch in aquaria. Although the exact date each egg was spawned was uncertain, this hatching time appears to be nearly correct for the Osage River. Paddlefish arrived in the spawning area on April 16, and spawning was seen through April 22. On April 26 almost all eggs were gone from the gravel bars. Of the eggs placed in aquaria, the last hatched April 28. In isolated pools where the water temperature was much higher, hatching appeared to take place more quickly.

The larva wriggled violently inside the capsule before hatching, then the caudal region broke free of the capsule. The attachment of the egg to the rock held the capsule, and the larva wriggled free. The larvae in unattached eggs required much longer to free themselves, and several died before more than the caudal region was free. In others that lived, the yolk sac appeared reduced considerably more than in fast-hatching individuals.

After the larvae became free they were swept away by the current or lay exhausted between rocks. Very soon they began a continuous erratic swimming from the bottom to the surface, seldom resting except when gliding down to the bottom. This was observed both in the river and in aquaria. The erratic movement in swimming was caused by the weight of the yolk sac. In 2 or 3 days enough of the yolk had been absorbed so that swimming became easier, and they were able to swim in a straight line. From the first few minutes after hatching these larvae swam continuously and never rested, although they touched bottom occasionally. The immediate swimming action served to remove them from

the gravel bars before flood waters receded and caused desiccation. The constant swimming in the flood waters present at spawning time swept them to deep water; then, apparently rather quickly, to the headwaters of the Lake of the Ozarks. Seining several days after spawning took place has never revealed small paddlefish in the spawning area.

A great many paddlefish eggs and some larvae were desiccated due to the rapidly falling water level on April 24–26. Both eggs and larvae were found on drying gravel bars during this period. Other eggs were recovered from under silt or floating free.

SECOND SPAWNING PERIOD

On April 29 and 30, 1960, another series of rains raised the water level 11 feet. Paddlefish were again abundant in the Osceola area on May 1. Water levels had receded little by May 5 when rains raised the level to 18 feet above the level of April 27. High levels remained through May 14. By this date there was no evidence of further spawning. No paddlefish were taken by snagging fishermen on May 15. During this period water temperatures were usually 59° to 60°F. On May 5 the water temperature was 64°F., but the flood waters of the day following lowered this to 60°F.

Slow recession of water levels during this flood allowed hatching of most eggs before the gravel bars were bared. Eggs were obtained off the gravel bars during this period with a dredge net (Turtox 105A50). Free-floating eggs and two larvae were obtained by hanging a small trawl net on bushes in the current below gravel bars. Several eggs obtained by both methods were hatched in an aquarium. However, viability of the loose and free-floating eggs was much lower than of those that had been attached to gravel.

EXTENT OF SPAWNING AREAS

On April 26, 1960, all the gravel bars and other possible spawning areas were visited to determine the available spawning area and its use. The areas were most abundant from the mouth of Weaubleau Creek downstream to the Brown Ford Bridge (numbers 1 through 7, Figure 1). This reach of stream appears to be desired for its extensive gravel bars, many of which are gravel islands in times of low water, interspersed with large deep pools. The pools would afford resting and feeding areas.

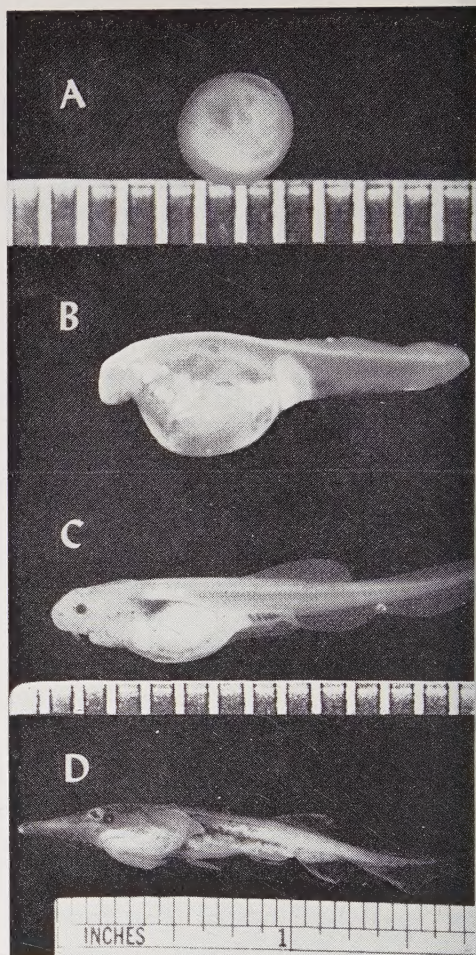


FIGURE 3.—Various stages in the development of the paddlefish. A.—Egg in early stages of development collected from a gravel bar. Graduations in millimeters. B.—Newly hatched prolarva. Prolarva 48 hours old. Graduations in millimeters. C.—Prolarva 48 hours old. Graduations in millimeters. D.—Paddlefish 29 days old. Failed to feed suffering oxygen deficiency and died.

Downstream from Brown's Ford Bridge, eggs or dead larvae were found on most spawning gravel bars down to Smart's Island (numbers 8, 9, 10, Figure 1). The bars in the vicinity of Belle Island also appeared suitable for spawning. No eggs were found on bars composed of large rubble or on boulders. However, the swifter current where these are the only remaining bottom materials might be a deterring factor.

DESCRIPTION OF THE EGG AND LARVAE

The average diameter of 19 fertilized eggs was 3.0 millimeters with a range of 2.7 to

imeters. The entire egg capsule was adhesive. Beneath this the blastoderm area was yellow and the yolk area was a light tan. The blastoderm never entirely covered the yolk (Figure 3A). Immediately prior to hatching about one-half of the yolk was still visible, and the white larva encircled the entire egg. Seven larvae preserved upon hatching were 8.1, 8.2, 9.3, 9.4, and 9.5 millimeters in total length. One dead larva 7.4 millimeters long was collected.

When hatched, the paddlefish larvae were recognized by the distinctive yolk sac which retained the appearance of the egg. At that time the head was large; eyes, rostrum, or barbels were not apparent; and the fins were differentiated (Figure 3B). However, in a 47-hour-old specimen the barbels began to be apparent. After 24 hours the barbel buds were easily seen with a 10 $\times$ magnification. By the third week the rostrum was developing rapidly. Some larvae were kept alive 5 weeks while their development and behavior were studied. One 29-day-old specimen which grew very rapidly attained a length of 47.9 millimeters and had a rostrum 7.8 millimeters long (Figure 3D).

DISCUSSION

Coker (1930) discussed the marked decline in the paddlefish fishery of the Mississippi River following construction of a dam at Keokuk, Iowa, in 1913. Barnickol and Starrett (1951) reported the much more drastic decrease which had occurred by 1946 when commercial catches had declined to only 9.58 percent in Missouri and 18.12 percent in Illinois of the 1899 catches. In this period a series of navigation dams was completed which impounded much of the river and caused silting in the canalized section. The heavy sand and gravel bottoms remaining were in the upper parts of the pools where the current was swift. The findings reported here would suggest that the loss of spawning areas was responsible for the decline in the

Mississippi River fishery. With the lack of good spawning areas, some paddlefish may fail to spawn. Others may choose less desirable areas where gravel and rock for attachment of the eggs are lacking and where a high proportion of eggs and larvae would fail to survive.

A proposed flood-control reservoir would cut off the paddlefish population of the Lake of the Ozarks from its spawning grounds. The dam for this reservoir would be at Kasinger Bluff, 1 mile upstream from Warsaw. If this is built, large catches might be made immediately downstream from the dam for a few years. However, alternate spawning areas would be extremely limited, and it is probable that there would be a gradual decline in the paddlefish population of the Lake of the Ozarks. If there are significant numbers of paddlefish in the impounded portions of the river when the dam is closed, a limited fishery might develop in the new reservoir and upstream to Osceola. Present plans are for the conservation pool level to extend to the downstream bend of Horseshoe Bend (Figure 1). This would leave a considerable extent of the best spawning areas previously mentioned available at normal levels. However, only 12 miles of stream would remain to Osceola Dam.

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Age and Growth of Walleyes in Clear Lake, Iowa, 1935 - 1957¹

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ABSTRACT

Interpretation of walleye (*Stizostedion vitreum vitreum*) scales by three investigators revealed some differences in detail, but the data derived appeared to be basically reliable. Most fish were collected in experimental gill nets. Lengths at annuli were calculated using straight-line relationship with an intercept of 3.26 inches, total length. Growth rate of a year class, as indicated by mean length at the third annulus, was negatively correlated with abundance of the year class ($r = -0.78$, 11 d.f.). Walford's growth transformation did not give an entirely satisfactory fit but gave a maximum length of 31.1 inches and a k of 0.836. Variations in these values with different treatment of the data were indicated. Fitting a Walford transformation to increments gave: $L_{t+1} = 28.8$ inches $(0.172) + 0.828 L_t$. The correlation coefficient, r , between the annual increment indexes and the mean May to September temperatures was 0.565. Adding April and October temperatures lowered the correlation. Instantaneous growth rates, i , decrease rapidly with age and with increased length. Several indexes to growth during calendar years using i values and Parker and Larkin's L^2 values, were tried, but the Hile increment indexes gave the best correlation with summer temperatures. Growth of female walleyes was faster than that of males.

INTRODUCTION

The walleye (*Stizostedion vitreum vitreum*) is one of the most important species of fish in Clear Lake. Cleary (1949) reported on an analysis of the age and growth as determined from scales collected in 1941, 1942, 1943, and 1947. Whitney studied the scales collected from 1948 through 1953 and Carlander those collected from 1954 through 1958. Correlation of data from scale analysis by the last two biologists has presented some problems which will be discussed later in this paper.

Scales were taken primarily from June through August each year from fish caught principally in experimental gill nets (with equal lengths of 1.5-, 2-, 2.5-, 3-, and 4-inch mesh, stretch measure). All lengths are reported as total lengths in inches (tip of snout to end of caudal fin, with lobes of the fin parallel and with the fish flat on a ruler). Scales were collected from an area just below the lateral line and at the end of the pectoral fin extended caudad. The scales collected through 1953 were read from wet mounts (Lewis and

Carlander, 1949), those since 1954 from plain impressions.

Stratified subsampling (modified from Trench, 1950) was used on the 1949 through 1952 collections, to provide samples of about 200 from each year. Additional samples were taken from the strata containing larger numbers because there was greater difficulty in reading them. Information from the subsamples was projected to the entire number in a stratum by application of the proportion of the subsample to the whole.

AGE CLASSIFICATION

The age-group and year-class composition of the walleyes was considered by Carlander, Whitney, Speaker, and Madden (1960). They found that abundance of year classes (Table 1) was related to fry stocking, with the most abundant year classes coming from years in which no fry were stocked.

TABLE 1.—Index of abundance of year classes of walleyes¹

Year class	Index	Year class	Index
1943	36	1951	9
1944	89	1952	15
1945	86	1953	8
1946	125	1954	11
1947	112	1955	4
1948	91	1956	5
1949	91	1957	8
1950	151		

¹ The 1947 through 1957 indexes were taken from Carlander, et al. (1960); the 1943 through 1946 indexes were computed in the same manner.

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TABLE 2.—Total length (inches) at capture of Clear Lake walleyes in each age group as assigned by three biologists

Age Group	1941-43, 1947 ¹		1948-53 ²			1954-58 ³		
	Number	Mean	Number	Mean	Range	Number	Mean	Range
—	—	—	7	7.94	7.1-7.5	6	5.52	5.1-5.8
49	9.72	286	9.68	6.9-13.5	31	8.86	6.4-10.9	
97	12.77	971	12.88	9.1-17.8	134	13.05	11.2-16.0	
77	15.57	515	15.94	12.8-21.0	171	15.84	12.9-19.5	
53	17.38	238	18.09	14.9-22.3	121	17.34	15.1-21.2	
26	18.95	50	20.27	18.0-22.8	105	18.46	14.8-22.8	
8	22.06	28	21.65	18.1-26.5	48	20.08	17.5-23.0	
2	22.4	12	22.58	21.3-26.8	33	21.60	17.9-25.1	
—	—	4	23.25	20.7-27.0	9	23.65	21.6-25.4	
—	—	2	26.75	26.0-27.5	5	24.02	20.8-26.5	
1	28.3	—	—	—	1	27.0	—	
1	28.5	—	—	—	—	—	—	
—	—	—	—	—	2	28.3	27.7-28.8	

¹ Cleary
² Whitney
³ Carlander

The average total lengths of walleyes in each age group (Table 2) show some variation among age groups older than age-group IV and suggest differences in the interpretation of scales on older fish by the different biologists. Differences in growth rates in the three periods may be responsible for some of these discrepancies but such differences would be expected to be more evident in the younger age groups since the older age groups overlap the periods. The differences in age-group composition for the three periods probably indicate differences in interpretation of the number of annuli on the older fish. Annuli on older fish may be more easily recognized from scale impressions than from the scales. In the scales read by Carlander, 14.7 percent were interpreted as having six or more annuli, compared to 2.2 and 3.8 percent in those read by Whitney and Cleary.

The criteria for recognition of annuli were crowding of circuli, a wide space between annuli of circuli, particularly at the anterior-lateral angle, and anastomosis of circuli on the lateral fields. The last criterion was considered the most significant but all criteria involved some subjectivity. All scales were read without knowledge of the sizes of the fish at capture.

RELATIONSHIP BETWEEN BODY LENGTH AND SCALE LENGTH

In estimating body lengths at various periods in life from the scale measurements, it is customary to employ a regression based on body and scale lengths of fish at time of capture. Cleary (1949) used the following relationship based upon 215 Clear Lake walleyes: standard length (millimeters) = $35.7(\text{millimeters} + 2.33 \text{ anterior scale radius} \times 27)$. Carlander (1945) and Eschmeyer (1950), who

had the two largest samples among the studies so far reported for the walleye, agreed that the relationship could be best described by S-shaped curves. In the present study, scale radii and body lengths of 1,209 walleyes collected from 1948 to 1953 were used to describe the regression. Since the smallest walleye included was 6 inches long and only 58 were less than 9 inches, no curvilinearity near the origin is apparent (Figure 1). There is some change in the slope for walleyes over 22 inches long, but deviations from a straight line are not great considering that the upper part of the curve is based on only a few fish.

The relationship between scale radius and

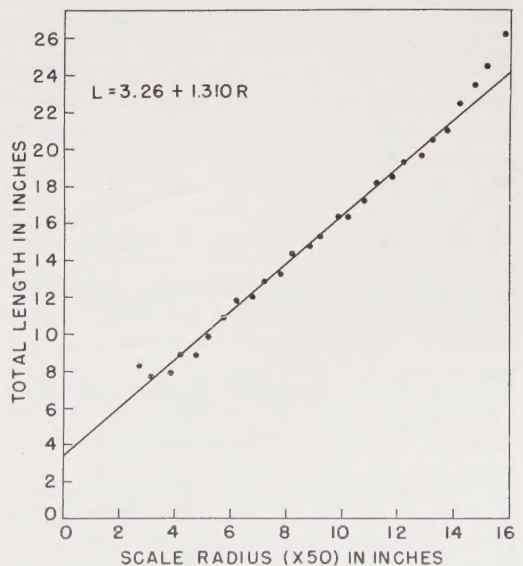


FIGURE 1.—Relationship between total length in inches and scale radius (x50) in inches of walleyes from Clear Lake, Iowa. Dots represent mean scale radii for walleyes in half-inch size groups.

TABLE 3.—Mean calculated total lengths (inches) at each annulus for the 1935 to 1957 year classes of walleyes in Clear Lake, Iowa

Year class ¹	Number by age group ²	Length at each annulus										
		1	2	3	4	5	6	7	8	9	10	11
1935A	0, 0, 0, 0, 0, 1	7.0	10.2	14.7	18.0	20.7	22.7					
1936A	0, 0, 0, 0, 0, 5, 0, 0, 0, 0, 1	8.8	13.4	17.0	19.6	21.8	22.8	25.8	26.6	27.2	27.8	28.2
1937A	0, 0, 0, 4, 21, 0, 0, 0, 0, 1	7.7	11.8	14.6	17.0	18.9	24.2	25.1	26.1	27.0	28.0	
1938A	0, 0, 2, 26	7.5	11.7	14.3	16.7							
1939A	0, 38, 5, 5	6.6	10.5	13.5	17.9							
1940A	8, 0, 6, 0, 0, 0, 2	7.0	10.6	13.3	16.6	19.0	21.0	22.0				
1941A	0, 1, 0, 0, 0, 2	6.6	10.2	13.6	16.7	17.9	19.1					
1941B	0, 0, 0, 0, 0, 0, 0, 2	7.6	12.6	15.8	18.1	20.3	21.6	22.6	23.4			
1942A	1, 0, 0, 0, 5	6.9	10.3	14.2	16.9	19.0						
1942B	0, 0, 0, 0, 0, 0, 5	7.0	12.0	16.1	19.2	20.7	21.9	22.8				
1943A	0, 0, 0, 18	6.5	11.0	14.5	17.0							
1943B	0, 0, 0, 0, 1, 6, 0, 0, 1	7.4	12.6	16.5	19.4	21.0	22.2	25.6	26.4	27.1		
1944A	0, 0, 64	6.8	11.8	14.7								
1944B	0, 0, 0, 16, 15, 4, 2, 2, 1	7.1	11.8	15.6	17.9	19.8	20.9	22.1	22.8	25.6		
1945A	0, 58	6.9	11.8									
1945B	0, 0, 25, 65, 5, 2, 5	7.2	11.8	15.3	17.4	19.2	20.4	21.2				
1945C	0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1	7.6	11.6	16.3	19.0	21.5	22.7	23.8	25.0	26.0	26.8	27.7
1946A	40	7.0										
1946B	0, 93, 147, 72, 11, 12	7.0	11.4	14.6	16.9	19.6	20.8					
1946C	0, 0, 0, 0, 0, 0, 0, 0, 3, 0, 0, 1	7.3	11.2	15.4	18.3	20.3	21.6	22.8	23.7	24.3	25.8	26.6
1947B	24, 346, 128, 29, 10, 4	7.0	11.6	14.9	17.3	19.1	21.4					
1947C	0, 0, 0, 0, 0, 0, 0, 1	7.5	12.5	16.2	18.9	20.4	21.9	23.2	24.3			
1948B	73, 116, 16, 28, 8	6.5	11.7	15.1	17.2	18.6						
1948C	0, 0, 0, 0, 0, 4, 4, 1, 2, 1	7.6	11.9	15.1	17.3	18.8	20.0	21.5	23.9	24.3	26.7	
1949B	16, 61, 69, 28	6.9	10.3	13.6	16.8							
1949C	0, 0, 0, 0, 5, 1, 2, 3	7.6	11.4	14.6	17.1	19.0	20.6	21.3	23.0			
1950B	103, 340, 129	6.6	10.3	14.1								
1950C	0, 0, 0, 40, 19, 17, 26, 4	7.3	11.1	15.0	17.3	19.2	20.6	21.5	22.9			
1951B	49, 15	8.0	12.9									
1951C	0, 0, 13, 12, 15, 19, 1	7.7	11.6	15.0	16.7	18.1	19.2	24.0				
1952B	21	7.3										
1952C	0, 82, 110, 41, 58, 7	7.5	11.4	14.6	16.5	17.6	19.8					
1953C	1, 8, 14, 21, 8	7.5	11.6	14.6	16.7	18.0						
1954C	16, 38, 33, 7	7.3	12.4	15.3	17.0							
1955C	6, 4, 1	7.5	12.4	15.6								
1956C	5, 2	6.9	9.7									
1957C	3	7.3										
Average		7.0	11.3	14.7	17.1	18.9	20.7	22.0	23.8	25.3	27.0	27.5
Number of specimens		3,079	2,713	1,511	749	337	156	72	25	12	5	3

¹ A: from Cleary (1948), transformed to total lengths in inches and to body-scale intercept at 3.26 inches. B: by R. R. Whitney. C: read by K. D. Carlander.

² For example: for 1936A there were 5 age-VI and 1 age-XI walleyes.

body length might not be the same for each year class sampled or for each year of their capture. To test year classes and years of collection with equal precision requires equal numbers in the subclasses. By random selection among the possible samples with adequate numbers available in the 1948 to 1953 collections, the 1946, 1947, and 1948 year classes caught in 1949, 1950, and 1951 were selected for study. Scale radii and body lengths were converted to logarithms (as recommended by

Mottley, 1942). No significant differences between year classes ($F = 0.85$ with 2, 3 d.f. or years of capture was indicated ($F = 0.4$ with 2, 3 d.f.). The interaction was also not significant ($F = 1.54$ with 4, 80 d.f.). A single regression therefore appears to be suitable for use with walleyes of different year classes collected in different years. The following regression based on 1,209 walleyes was used: total length (inches) = 3.26 inches + 1.31 anterior scale radius (x50). Estimated

growth in early years were made with a nomograph in the manner described by Carder and Smith (1944), with 3.26 inches as the intercept.

ESTIMATES OF GROWTH HISTORIES

The lengths at various annuli, as computed from the samples collected in different years of life, showed considerable variation in fish of the same year class. Lee's phenomenon of apparent change of growth was not evident in any of the data, but instead there was an apparent tendency for each fish to grow faster in early years than when collected at younger ages. Missed annuli in a few of the older fish could account for this trend. The computed lengths of some older fish suggest undetected annuli where it is not possible without bias to identify marks as annuli.

The variation was not only among the mean lengths as computed from fish collected in different years, but also among the lengths for fish collected in the same year. For example, the calculated lengths at the first annulus for 28 age-group-IV fish collected in 1953 ranged from 5.9 to 8.3 inches; at the second annulus, from 8.9 to 12.2; at the third, from 10.6 to 15.4; and at the fourth, from 14.5 to 16 inches. The standard deviations were respectively 0.51, 0.76, 0.75, and 1.10 inches.

In view of this wide variation in estimates of length within a given year class, it is difficult to draw general conclusions concerning growth of the various year classes (Table 3). It is evident that the growth rate has not changed greatly over the period of study, but the more abundant year classes (1952, 1950, and 1946) showed slower than average growth rates. The weighted mean lengths at the third annulus of the 1943 through 1955 year classes have a negative correlation ($r = -0.78$, 11 d.f.) with the indexes of abundance (Table 1). Many studies have indicated that higher population densities result in lower individual growth rates. It is not believed that densities of the walleye population, considering all age groups, have varied greatly but that the relationship between slow growth and abundant year classes indicates greater competition within the particular year class.

The calculated lengths as determined by the biologist are listed separately in Table 4 so that this source of variation can be observed. Some of the differences result from sampling variation; some from the fact that different age groups were read; some from

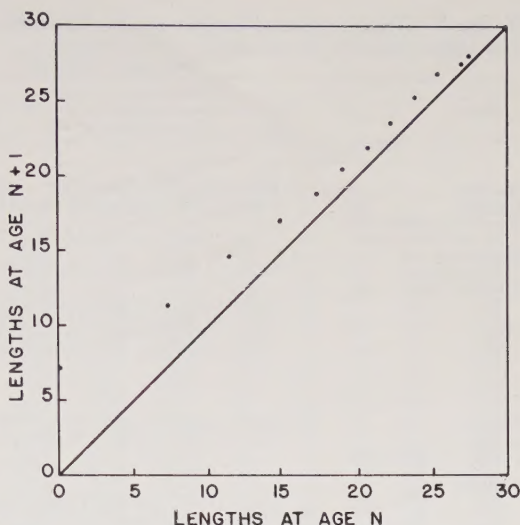


FIGURE 2.—Walford transformation of combined data, weighted means at each annulus, for 3,079 Clear Lake walleyes, collected 1941 to 1958. The line represents the 45° slope.

failure to recognize annuli; and perhaps some from individual differences in the exact portion of the annuli measured.

Growth of walleyes in Clear Lake is almost the same as that reported for Spirit Lake, Iowa (Rose, 1951), and faster than that in Wisconsin, Michigan, Minnesota, and Ohio, but slower than in North Carolina, Tennessee, and Virginia (Carlander, 1953).

Walford (1946) presented a method of describing fish growth curves for ready comparison. Plotting of lengths at age n against lengths at age $n + 1$ (Figure 2) does not give as satisfactory a straight line for the combined Clear Lake data as for growth data given by Walford. The points for ages 5 through 10 lie approximately parallel to the 45° diagonal. The straight line fit by the least-squares method to all points gave a slope, k , of 0.836 and a maximum length of 31.1 inches, and the mean calculated lengths (Table 4) are approximated by starting with 7.02 inches and computing successive lengths with the formula:

$$L_{t+1} = 31.1(.164) + .836 L_t \text{ (Walford line } a \text{)}.$$

The deviations from the observed lengths are greatest, however, in the early years of life where the data are more complete and also more important. The points for ages 2 through 7 line up well (Figure 2) and a line fit only to these points gives:

$$L_{t+1} = 26.3(.220) + .780 L_t \text{ (Walford line } b \text{)}.$$

TABLE 4.—Mean calculated lengths (inches) at various years of life and growth data according to various Walford lines

Item	Annulus											
	1	2	3	4	5	6	7	8	9	10	11	12
	Age groups I–XII											
Number	3,079	2,713	1,511	749	337	156	72	25	12	5	3	27.5
Length	7.02	11.28	14.70	17.09	18.91	20.65	21.98	23.79	25.25	27.02	27.5	27.5
Length of same fish at previous year		7.08	11.41	14.95	17.40	19.64	21.00	22.94	24.52	26.32	26.8	27.5
Summation of increments	7.02	11.22	14.51	16.65	18.16	19.17	20.15	21.00	21.73	22.43	23.13	23.8
Walford lines ¹												
a:	7.02	10.97	14.27	17.03	19.34	21.27	22.88	24.23	25.36	26.30	27.09	27.5
b:	7.02	11.26	14.56	17.14	19.15	20.72	21.94	22.89	23.63	24.21	24.66	25.5
c:	7.02	10.77	13.88	16.45	18.58	20.34	21.80	23.01	24.01	24.84	25.52	26.5
d:	7.02	11.23	14.42	16.84	18.67	20.05	21.10	21.89	22.49	22.94	23.29	23.8
	Age groups I–VII											
Number	3,054	2,688	1,486	724	312	131	47					
Length	7.02	11.27	14.68	17.03	18.77	20.41	21.46					
Length of same fish at previous year		7.08	11.39	14.91	17.29	19.24	20.54					
Walford lines ¹												
e:	7.02	11.27	14.52	17.00	18.90	20.35	21.46					
f:	7.02	11.24	14.41	16.79	18.57	19.91	20.91					

¹ See text.

Growth computed from this line fits well through the first 7 years but underestimates sizes in later years, and several of the walleyes examined were larger than the theoretical maximum length. In these two cases the Walford lines were fitted to the mean computed lengths at each annulus and represent the absolute growth curve, as defined by Rounsefell and Everhart (1953, p. 313). However, if the annual increments are computed by using only those fish which complete the year of life (line 3 of Table 4), a somewhat different picture of the growth rate is presented. The calculated lengths of the older fish at each annulus are longer than those of fish with that annulus being the last. This situation is the reverse of that found with Lee's phenomenon of apparent change of growth. It may indicate a tendency to record the last annulus a little farther in from the margin of the scale than the other annuli, or indicate the occasional missing of annuli on some of the older fish thereby giving the average computed lengths an upward bias. Perhaps the fish which live longer have a different growth pattern. While the absolute growth curve represents the average growth pattern in the population as a whole, it does not provide, at least in this case, the best information on such questions as the growth of a fish of a certain size and age. Annual increments are more meaningful in such situations.

A Walford line fitted with lengths at age n from the same fish as used in computing lengths at $n + 1$ is the best line for comput-

ing the average next year's size for walleye of any given length:

$$L_{t+1} = 23.8(.172) + .828 L_t \text{ (Walford line fitted to all fish)}$$

If only the points for ages II to VII are used, the line has the formula:

$$L_{t+1} = 24.4(.243) + .757 L_t \text{ (Walford line fitted to ages II to VII)}$$

Since the data for the fish beyond age VII do not line up well with the others and scales may be subject to greater error in interpretation, it might be well to disregard these older fish. Elimination of all fish beyond age VII reduces the sample by only 0.8 percent and leaves a more homogeneous sample. The least-squares fit of the Walford line to these data gives:

$$L_{t+1} = 25.0(.236) + .764 L_t \text{ (Walford line fitted to ages I to VII)}$$

If fitted only to the fish which complete a given annual increment:

$$L_{t+1} = 23.9(.25) + .75 L_t \text{ (Walford line fitted to complete increments)}$$

This suggests a different growth pattern for those fish which exceed 25.0 or 23.9 inches or a difference in the ability to read the scales.

GROWTH IN VARIOUS CALENDAR YEARS

Mean annual increments in length decrease with age. For the purposes of comparing growth in various calendar years only the walleyes in age-groups I through VII were used (Table 5). In general, increments at differ-

TABLE 5.—Mean annual increments in inches in each year of life of Clear Lake walleyes of age-groups through VII by calendar years, 1935 to 1957¹

Calendar year	Year of life						
	1	2	3	4	5	6	7
1935	7.0	—	—	—	—	—	—
1936	8.8	3.2	—	—	—	—	—
1937	7.7	4.2	4.5	—	—	—	—
1938	7.5	4.1	3.5	3.3	—	—	—
1939	6.6	4.2	2.8	2.6	2.7	—	—
1940	7.0	3.9	2.6	2.4	2.3	2.0	—
1941	6.6	4.0	2.2	2.3	1.9	1.1	—
1942	6.9	3.6	2.7	2.5	—	—	—
1943	6.8	4.3	3.3	3.2	—	—	—
1944	6.9	4.7	4.0	3.1	2.4	—	—
1945	7.1	4.9	3.6	2.9	1.2	2.0	—
1946	7.0	4.7	3.3	2.2	1.8	1.2	1.0
1947	7.0	4.4	3.6	2.1	1.7	1.2	—
1948	6.6	4.6	3.2	2.0	1.5	1.2	0.9
1949	6.9	4.9	2.9	1.9	1.6	0.9	—
1950	6.7	3.5	3.3	2.0	1.3	1.0	0.6
1951	7.9	3.6	3.2	2.1	1.3	1.3	0.9
1952	7.5	4.1	3.8	2.7	1.5	1.1	—
1953	7.5	3.9	3.4	2.3	1.9	1.2	—
1954	7.3	4.1	3.2	2.0	1.6	1.5	1.1
1955	7.5	4.8	3.3	1.8	1.3	1.2	0.9
1956	6.9	4.5	3.0	1.9	1.2	1.1	0.9
1957	7.3	3.2	2.6	2.0	1.2	1.0	1.6
Weighted mean	7.17	4.15	3.24	2.36	1.67	1.27	0.99

Numbers of specimens as in Table 3.

For a given calendar year show similar variations from the average. For example, 1950 increments were below average for except the third year of life. Failure of all age groups to show the same trends from year to year may be the result of (1) actual difference in growth conditions for fish at different sizes; (2) sampling variation, since the age groups are represented by only a few specimens; (3) misinterpretation of a few outliers; and (4) differences in measuring length by different biologists. There are several years in which the increments are about equally balanced between above and below average and thus do not show a consistent trend, e.g., 1940 and 1947. They may indicate years of near average growth.

An index to growth in each calendar year was derived (Table 6) by the method of Hile (1941). These data indicate slower growth since 1946 than in most previous years. In general, the growth appears to be better in warm summers. The correlation coefficient between the growth indexes and the mean May-to-September temperatures is 0.565 (significant, 1 percent level; 21 d.f.). Inclusion of the April and October temperatures lowered the coefficient to 0.387. The correlation between the indexes of abundance of year classes (Table 1) and these growth indexes is not significant.

Instantaneous growth rates in length, i , can be readily determined (Ricker 1958, p. 192).

TABLE 6.—Mean temperatures and growth indexes of walleyes in Clear Lake for the calendar years 1935 to 1957 (see text)

Year	Mean temperatures in °F.		Hile index	<i>i</i> indexes			
	April– October	May– Sep- tember		Type 2	Type 3	Type 4	<i>L</i> ² type index
1935	59.9	65.6	104	77	99	—	—
1936	62.9	70.1	127	164	96	—	135
1937	63.9	70.0	126	102	108	130	199
1938	62.5	66.7	118	115	106	143	209
1939	62.6	68.7	105	81	103	108	197
1940	61.2	66.1	101	99	108	106	165
1941	63.6	68.3	90	77	93	82	146
1942	60.8	64.8	94	79	96	76	149
1943	59.9	65.2	106	146	122	129	186
1944	60.2	66.0	111	135	123	137	200
1945	58.4	62.7	104	123	112	122	191
1946	60.7	64.1	97	102	101	103	163
1947	61.9	66.1	96	98	97	110	174
1948	61.9	66.7	91	87	93	103	155
1949	61.9	66.9	91	71	86	74	151
1950	58.0	62.9	84	72	83	79	134
1951	58.1	63.5	94	104	94	80	145
1952	60.1	65.7	100	112	101	105	170
1953	60.8	66.2	98	102	100	88	164
1954	60.4	65.3	95	98	102	91	156
1955	63.4	68.3	95	106	95	90	148
1956	61.0	65.7	89	80	91	81	142
1957	59.9	65.2	86	81	91	74	144

Since growth in length is not exponential, i is not constant over any large range of age or size (Figure 3). The decrease in i value with increase in length or age is fairly regular and is approximately defined by a straight line

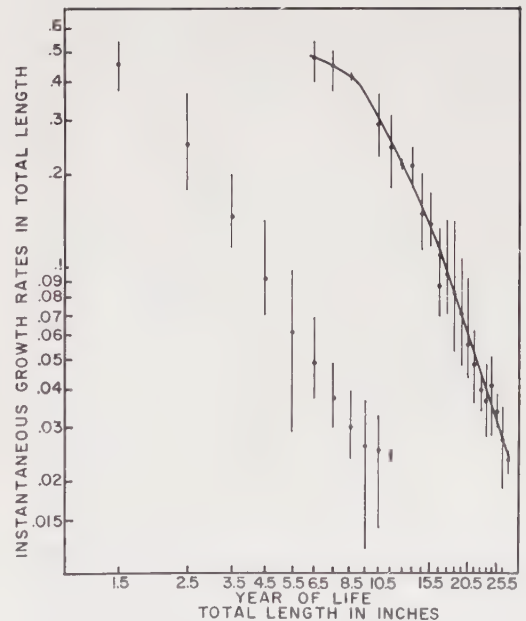


FIGURE 3.—Instantaneous growth rates, i , by year of life (to left) and by size classes by inches (to right) for Clear Lake walleyes. Vertical lines indicate range, and dots indicate mean value of i .

when transformed to a logarithmic scale. The *i* value for the second year of life is not in line with the others. Deviations of the values for the 11th and 12th years may be the results of errors in scale reading.

Several attempts were made to devise a better index to growth in various calendar years on the basis of instantaneous growth rates as follows:

1) Instantaneous growth rates arranged by year classes and year of growth (as were increments in Table 5) give a slightly greater agreement of above or below average values of *i* in a calendar year than was true of the length increments, but the difference is probably not significant.

2) The *i* values for each year class at each age were adjusted to a mean value of 0.1 by subtracting from each value a correction factor (mean *i* for the year of life minus 0.100). For example, the mean value for the third year of life is 0.254 and therefore 0.154 was subtracted from the *i* values at the third year for each year class. The adjusted *i* values for a given calendar year were then averaged to get an index of growth (Type 2 in Table 6). The variance (and range) of the *i* values was much greater in the early years of life and therefore deviations from the mean in the first year might have a numerical value to over-balance deviations in later years of life.

3) Another adjustment was made by dividing each *i* value by the mean *i* for that year of life, thus converting to a percentage index (Type 3 in Table 6). The variance was greater at the older ages.

4) Larkin, Terpenning, and Parker (1957) point out that size-specific instantaneous growth rates give a truer measure of growth. The *i* values were therefore grouped according to average size at the beginning of the year and were adjusted to a mean value of 0.1 as in method 2 except that the mean value at each length, as determined from the line in Figure 3, was used instead of the mean value at each age (Type 4 in Table 6).

Parker and Larkin (1959) developed another method of describing fish growth which takes into account the fact that size is an important criterion for physiological opportunity for growth. By selecting the proper power, *z*, of length, the annual increments can be made independent of length and a plot of L_{t+1}^z on L_t^z will therefore be parallel to the 45° diagonal. This concept was adopted in the development of a fifth growth index. With the data on age-groups I through VII

TABLE 7.— $L_{t+1}^{2.3} - L_t^{2.3}$ values for each year of life of Clear Lake walleyes of age-groups I through by calendar years, 1935 to 1957

Calendar year	Year of life					
	1	2	3	4	5	6
1935	88	—	—	—	—	—
1936	149	121	—	—	—	—
1937	106	216	275	—	—	—
1938	103	180	266	287	—	—
1939	77	183	176	257	293	—
1940	88	146	168	205	260	251
1941	77	151	134	187	184	140
1942	85	132	157	222	—	—
1943	82	177	236	249	—	—
1944	85	173	264	244	234	—
1945	91	207	240	258	122	225
1946	88	201	223	189	191	127
1947	88	182	245	190	190	146
1948	77	193	207	174	169	146
1949	85	204	201	157	153	103
1950	79	133	223	173	137	123
1951	116	138	189	179	137	148
1952	103	185	236	220	142	131
1953	103	167	226	197	177	112
1954	97	178	207	165	163	163
1955	103	220	213	147	123	135
1956	85	210	210	157	110	114
1957	97	112	190	169	113	107
Unweighted mean	94	173	214	201	170	145

of the Clear Lake walleyes, $z = 2.3$ when arrived in the manner of Parker and Larkin (1959, page 727). When all age groups were used, $z = 3.1$ gave a better fit.

The $L_{t+1}^{2.3} - L_t^{2.3}$ values for each year of life at each year of life (Table 7) may be averaged to give an index to growth in calendar years (L^z type in Table 6). The first increments deviate from the other years and may indicate another stanza of growth suggested by Parker and Larkin (1959). Otherwise, values and their variances show little correlation with increased age and therefore can be averaged more conveniently than instantaneous growth rates. The values averaged show a greater tendency to agree with the given calendar year than do the actual increments (Table 5).

Which set of indexes best represents the differences in growth in various calendar years is not known, but types 2, 3, 4, and 5 did not give as good a correlation with summer temperatures as did that of Hile. Types 1 of May–September temperatures and various indexes were: for Hile, 0.56; for number 1, 0.17; for number 3, 0.01; for number 4, 0.01; and for L^z , 0.13. The Hile index is also more direct and more easily interpreted than the others.

GROWTH OF MALE AND FEMALE WALLEYES

Sex data were not available for most of the fish included in the growth study, but the collection was made during the 1953 spawning

TABLE 8.—Average calculated total lengths in inches for each annulus and average annual increments in inches for male and female walleyes, Clear Lake, Iowa, 1953

		[Number of fish in parentheses]						
		Annulus						
		1	2	3	4	5	6	7
Related lengths								
Male	7.4	11.8	15.5	17.7	19.1	20.1	22.5	
Female	7.4	11.9	15.9	19.0	21.4	22.5	23.5	
Annual increment								
Male	7.4	4.4	3.7	2.2	1.3	0.9	0.9	
	(117)	(117)	(117)	(93)	(55)	(14)	(2)	
Female	7.4	4.5	4.0	2.7	1.6	1.0	0.7	
	(22)	(22)	(22)	(15)	(10)	(9)	(6)	

season when the sex was easily determined. These fish were all mature at the time of collection, and comparisons of growth may not be entirely valid because there are differences in age at maturity. The youngest of each sex were age-group III. There was one age-IX and one age-X female, and age VII was the maximum age of the males in the group. Considering only ages III through VII, 88 percent of the males and 59 percent of the females were age III to V. The males appear to grow faster than the females in the third through the sixth year (Table 3). Most studies have indicated that female walleyes grow faster and live longer than the males.

DISCUSSION

Frequent mention has been made of discrepancies and possible errors in the reading of some scales, but the results are believed to be basically reliable for the following reasons: There were some differences between the average growth rates as determined by each of the three biologists, but there was general agreement. The average calculated lengths at first annulus as determined by the three averaged by 0.6 inch and those at consecutive annuli by 0.6, 0.2, 0.8, 1.1, and 1.7 inches. Some of these differences may reflect actual changes in growth over the years.

The relative abundance of year classes, as determined from annuli on scales, was fairly consistent from year to year. For example, the 1952 year class was the most abundant in the year in the 1954 through 1957 collections, or as age-groups II, III, IV, and V. The 1950 year class was the most abundant year in the 1951 through 1953 collections, read by Whitney, and was more abundant in the 1949 or 1951 year classes in each collection from 1954 through 1958, read by Carlander.

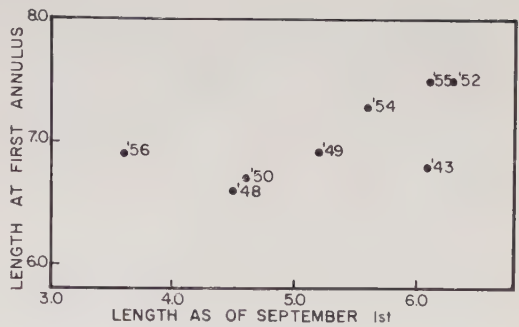


FIGURE 4.—Relationship between total length of young walleyes (inches) on September 1 and at time of first annulus formation in various years 1943–1956, Clear Lake, Iowa.

The calculated growth rates for the various year classes showed a negative correlation with year-class abundance. Such a correlation might be expected from various experiments and other observations indicating that for fish in general growth rate usually decreases as population density increases.

Calculated lengths for fish in year-classes 1948 to 1952, derived separately by Whitney and Carlander, showed some discrepancies (Table 3), but the rankings of these year classes at each year of life were very similar within each set of data.

Calculated increments, in general, showed similar trends for various calendar years (Table 5). These increments also showed a positive correlation with summer temperatures, a relationship which seems biologically sound.

The computed lengths for the first annulus for various year classes in general vary in the same way as do the average sizes of young-of-the-year on September 1 as determined by seining along shore (Figure 4) (data from Ridenhour, 1960). The correlation coefficient, r , was 0.57 (6 d.f.), but was not significant at the 95 percent level. It might be pointed out that the two greatest deviants, 1943 and 1956, are based upon smaller samples than the other points.

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Modification of the Microhematocrit Technique with Trout Blood

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ABSTRACT

Commercial and laboratory-prepared capillary tubes for hematocrit were tested. A 10 percent solution of heparin was found to be best for the preparation of treated capillary tubes. For examination of trout blood laboratory-prepared capillary tubes were found to be superior to commercial tubes which are designed for human blood. Sharp, pointed heparinized capillary tubes were used with good results for collecting blood from the heart without killing the examined fish. Hematocrits determined directly in such tubes were found to have the same value as those prepared in other ways.

INTRODUCTION

The hematocrit, or the percentage of red cells in blood, is rapidly becoming the method most frequently used for the detection of anemia. Hematocrit is extremely reliable and can be easily and rapidly performed with fish blood (Snieszko, 1960). Capillary tubes treated with heparin and all capillary instruments required for the performance of microhematocrits are commercially available. It has been found, however, that due to the rapid and unique way in which fish blood coagulates (Wolf, 1959), clots frequently are formed in heparinized capillary tubes prepared for use with human blood, and in such cases readings may be 7 to 18 percent higher than a true reading (Snieszko, 1960). It would seem likely that the modification of the anticoagulant would be conducive to greater accuracy. With this thought in mind, several different anticoagulants and various concentrations were tried. The method of collecting blood from fish has also been investigated. This subject was reviewed recently by Snieszko (1960). Most frequently blood is collected from fish by severing the caudal peduncle, but this method is prohibitive if valuable fish or large numbers of fish are examined. The simplest method of sampling would be to collect blood with a microhematocrit capillary tube used as a blood-letting instrument and as a collecting vessel without killing the fish. Similar procedures have been reported by Perkins (1957) and Suye (1958). Such a procedure was tested, and was very satisfactory, and is described here. The method described by Schiffman (1959)

was not convenient when pointed capillary tubes were used instead of hypodermic needles. Schiffman's method also requires transfer of blood from a syringe to a capillary tube for determination of hematocrit.

METHODS

Different anticoagulants at various concentrations were used to coat the inside of plain capillary tubes 1.2 to 1.4 by 75 millimeters in size. The tubes were coated by placing one end into a vial of the anticoagulant and tilting the capillary tube to a horizontal position. After the tube was over half full, it was removed from the stock vial and appressed end to end with the next plain tube and turned to a vertical position. The anticoagulant thus flowed from the upper tube to the lower tube, coating both tubes uniformly.

After coating, the capillary tubes were usually freed from excessive fluid by light centrifuging (with the blunt end down) and then allowing them to stand overnight in an open dry container. The blood samples were taken in the following manner. The tubes were partially filled with blood by cutting off the caudal peduncle and filling them with the emerging blood. Next, the tubes were sealed, either in a flame or with modeling clay, and centrifuged.

After centrifuging, each pair of tubes was examined to determine the volume of red cell pack and then broken and emptied to ascertain the presence of clot. After eliminating the tubes with the unsatisfactory concentrations of anticoagulants by comparing the results from several fish, the one which seemed to work best was compared with the commercially available treated tubes by sampling 6 rainbow trout (*Salmo gairdneri*), 15 brown trout (*Salmo trutta*), and two lots of

¹Trainee at the Eastern Fish Disease Laboratory during 1959-60.



FIGURE 1.—Collection of blood by means of a pointed microhematocrit capillary tube from the heart of a trout.

15 brook trout (*Salvelinus fontinalis*). More of the brook trout were used because there were difficulties caused by coagulation of blood in this series of tests. The hematocrit was recorded and the presence of clot ascertained. Presence or absence of hemolysis was also noted.

Pointed, heparinized capillary tubes were prepared and tested in order to develop a method of withdrawing blood directly (into the capillary tubes) without injuring the fish. Such capillaries were made by fusing two plain tubes end to end in a pinpoint flame and drawing the soft glass out to a constriction. The tubes were then broken off so that the sharp constricted end had an inside diameter of about 0.5 millimeter. The anticoagulant was introduced in exactly the same fashion as in the plain tubes except that the pointed end of the tube half filled with anticoagulant was placed in the wide end of the next tube before being raised to a vertical position.

To withdraw a blood sample with the pointed tube the fish was anesthetized in a 1:10,000 solution of M.S. 222² and blotted by wrapping in a paper towel. The operculum was lifted with a glass stirring rod and the site of the puncture blotted lightly with absorbent tissue. The pointed tube was then used to puncture the membrane at the back of the branchial chamber and penetrate the heart, *truncus arteriosus*, or associated structures (Figure 1). The method is similar to that described by Perkins (1957) and Suyehiro (1958).

As the puncture was made blood surged

TABLE 1.—The effect of various anticoagulant coated capillary tubes on trout blood hematocrit

Treatment of capillary tubes	Average hematocrit	Clotting time
Commercial heparinized ¹	44	
Anticlot ²	42	
15 percent DETA ³	41	
10 percent potassium oxalate	37	
10 percent oxalate, ammonium oxalate mixture	40	
25 percent sodium fluoride	38	
25 percent sodium citrate	33	

¹ Capillaries from Arthur H. Thomas Co., Philadelphia, Pa., and A. S. Aloe Co., St. Louis, Mo., used interchangeably.

² Heparin anticoagulant solution available from Clinco Laboratories, Los Angeles, Calif.

³ Dipotassium ethylenediamine tetraacetate.

into the capillary tube. If the puncture was misoriented, the tube picked up some body fluid which resulted in a false reading. After the sample was drawn, the tubes were sealed and centrifuged in the usual manner.

Thirty yearling trout were checked by making a heart puncture with the capillary tube and then immediately cutting off the capillary peduncle and sampling blood from this location. The number of fatalities resulting from the method of heart puncture was determined by sampling 50 fish at the raceway. After a sample was taken, the caudal fin was clipped and fish were returned to the raceway. The raceway was then checked each morning for fatalities in the marked group.

An additional 10 fingerlings of the current year class (50 per pound) were also sampled to see whether they could survive this method of blood sampling. They were held overnight in a small trough and checked for fatalities.

RESULTS

The results of tests with the various anticoagulants are presented in Table 1. All anticoagulants except heparin and Anticlot were used at the lowest concentrations which completely prevented clotting. It is evident that at these concentrations all anticoagulants, except heparin and Anticlot, apparently caused some shrinkage of erythrocytes, which would explain the differences in hematocrit values obtained in heparin-treated capillaries as compared with the other anticoagulants. In this particular series of tests no clots were observed in the commercially prepared heparinized capillaries. This result was unusual.

The results of the comparison of commercial heparinized capillary tubes and tubes treated with a 10 percent solution of heparin are given in Table 2. It is evident that

² Tricaine methanesulfonate (Sandoz).

TABLE 2.—Comparison of commercially prepared heparinized capillary tubes and capillary tubes coated with 10 percent aqueous solution of heparin used on three species of trout

Species of fish	Type of capillary tube	Hematocrit				Hemolysis (percentage of tubes)
		Mean	Mean deviation	Presence of clotting		
				Trace (percentage)	Distinct (percentage)	
Bow trout	Commercial	45.8	3.35	8.3	41.6	16.7
	10% solution	44.8	3.55	—	—	16.6
Rainbow trout	Commercial	38.4	2.48	36.6	36.6	—
	10% solution	37.7	2.56	10.0	—	—
Brook trout Series I	Commercial	55.5	3.17	3.3	43.3	23.3
	10% solution	56.6	3.60	—	2.6	—
Brook trout Series II	Commercial	59.1	4.57	6.65	—	—
	10% solution	58.6	5.76	—	—	3.3

Laboratory-prepared tubes treated with 10 percent heparin are superior to the commercial tubes in preventing clotting of trout blood. The differences in hematocrit values obtained in both types of capillary tubes were significant.

In another test blood was collected from the same trout first by heart puncture with a capillary tube. This was followed immediately by sampling blood, in duplicate, from severed caudal peduncle. It is evident from the data presented in Table 3 that the reliability and accuracy of both methods is the same.

There were only two mortalities among the trout sampled and fin-clipped at the race. Ten trout, which were held in a small tank and sampled three or more times each, showed no mortalities. The method was also used on 10 fingerlings of the current year class of rainbow (50 per pound) with no mortalities.

CONCLUSIONS AND RECOMMENDATIONS

The results of these tests indicate that, on trout blood, plain capillary tubes coated internally with a 10 percent solution of heparin are superior to the commercially prepared tubes which were tested. Hematocrit values obtained with blood taken by heart puncture using pointed heparinized tubes compare favorably with the values of samples taken from severed caudal peduncle. This finding is important because the losses among examined fish can be kept at an insignificant level.

The following recommendations are made on the basis of the results described in this report:

(1) Laboratory-prepared capillary tubes treated with 10 percent heparin give very satisfactory results with almost no clotting and little hemolysis and should be used in preference to commercial tubes which are made for human blood. (2) Heparin solution

is stable but should be kept in a refrigerator and discarded if it becomes turbid. (3) After treating with a 10 percent heparin solution tubes should be briefly centrifuged to remove excess liquid which may produce solid heparin rings upon drying. (4) Heparin should not be exposed to heat in drying capillary tubes. Drying for 1 day at room temperature or in an incubator at 30–35° C. is entirely sufficient. (5) Whenever possible, blood samples should be collected by means of pointed tubes directly from the heart of anesthetized fish. (6) Only one blood sample should be taken from each fish on any one date to prevent complications and possible incorrect hematocrit value. (7) The area of puncture should be kept free from water to avoid dilution of the blood sample. (8) If any clear fluid enters the capillary tube or if there are any difficulties in filling the tube almost instantly, the sample should be discarded and another fish examined. (9) After collecting the sample and before sealing, tap the open end of the tube sharply to force the sample below the level of the constriction. This assures good exposure of the entire sample to anticoagulant action. (10) If other tests in addition to hematocrit are contemplated, blood could be collected into a 150-millimeter (or double-length) heparinized capillary tube. Then the tube can be cut in two,

TABLE 3.—Hematocrit values of blood samples taken by means of pointed capillary tubes by heart puncture and blood collected from severing the caudal peduncle

Method of blood sampling	Hematocrit		Mean deviation between duplicate hematocrits
	Mean	Mean deviation	
Cardiac puncture by pointed tubes	46	4.4	—
Severing caudal peduncle	46	4.1	1.33

one half used for hematocrit, the other half for determination of hemoglobin or other tests. (11) The ability to make a quick neat puncture requires practice. If difficulty is encountered in drawing blood samples, it will be advantageous to dissect out the heart and associated structures through the puncture site and then resume sampling on other fish using the dissected specimen as a visual example.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to Dr. John Halver³ and Mr. E. Hesser for critical read-

³ Dr. Halver recommended the use of M.S. 222 diluted not 1:10,000 but 1:20,000. This would permit safe keeping of anesthetized fish for much longer without danger of killing. However, in the authors' opinion rapid anesthesia is desirable because a prolonged keeping of fish in anesthetizing solution is likely to change hematocrit readings caused by partial asphyxia.

ing of the manuscript. Mr. Hesser doubts that preparation of heparinized capillaries is justified because blood clotting occurs in a relatively small percentage of commercial heparinized capillaries. In any case, pointed capillaries will have to be heparinized in the laboratory until they become commercially available.

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Physiological Effect of Organic Phosphorus Insecticides on Several Species of Fish¹

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ABSTRACT

Fish brain acetylcholinesterase is inhibited *in vivo* by organic phosphorus insecticides at concentrations of 0.1 mg/l and lower. The degree of inhibition is a function of the concentration of the insecticide, the extent of exposure, specific chemical nature of the inhibiting substance, and fish species. Species used were largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), golden shiner (*Notemigonus crysoleucas*), goldfish (*Carassius auratus*), and fathead minnow (*Pimephales promelas*). Fish removed from exposure to acetylcholinesterase-inhibiting insecticides, prior to reaching lethal limits, demonstrate the capacity for regeneration of this enzyme. The time required to regenerate the brain acetylcholinesterase to normal levels depends on the extent of the initial inhibition, the specific nature of the compound producing the inhibition, and the particular species. The curve of brain enzyme inactivation and recovery, as defined by percentage changes in normal activity, describes a physiological brain cholinesterase characteristic of the fish species. The period necessary to regenerate to normal activity may be longer than 30 days. By utilization of suitable fish species it is possible to demonstrate the presence of organic phosphorus insecticides in water at concentrations of 0.1 mg/l with exposure periods of 12 to 24 hours. Some compounds produce marked inhibition of brain enzyme activity in 6 hours. At 0.01 mg/l Guthion produces comparable *in vivo* inhibition of brain acetylcholinesterase in 12 hours' exposure in several species.

INTRODUCTION

The extremely widespread and often indiscriminate use of chemical agents for control of insect pests is rapidly becoming one of the classic examples of man's willful degradation of his environment. The potency of the newer compounds developed for insect control creates special conditions not only for the organisms against which they are primarily directed, but also for other organisms which may be exposed by direct application or by runoff into receiving bodies of water. The general hazard of pesticides to wildlife has been documented extensively by Rudd and Genelly (1956).

The practice of insect control by direct introduction of insecticides into the aquatic environment for destruction of aquatic larval stages poses a significant problem. With the development by insects of high tolerance or resistance to compounds such as DDT, new formulations developed for control purposes included the organic phosphorus insecticides (Nicholson, 1959). In many instances these compounds enter the aquatic environment not only by chance runoff from application to agricultural lands, but are introduced directly for insect control purposes (Davis and Gahan, 1957; Lewallen and Brydon, 1958).

Among the more popular formulations that have been used for this purpose are: Chlorothion, malathion, DDVP and Dipterex, which have been reported as producing 100 percent mortality of *Psorophora confinnis* larvae at concentrations of 0.0125, 0.1, 0.1, and 0.25 mg/l, respectively (Mathis and Schoof, 1957). Parathion has been used at concentrations of 0.01 to 0.1 mg/l in irrigation water in California for effective control of *Aedes* spp. (Gahan, 1957). In Florida, parathion at 0.5 and 1 mg/l eliminated all blackfly larvae (*Simulium* spp.) after a 5-minute treatment period along a stretch of 1.6 miles of two streams (Davis *et al.*, 1957).

The toxicity of organic phosphorus insecticides to fish life, as determined by standard bioassay procedures, is very high. Although generally not as toxic as the chlorinated hydrocarbons, some of the organic phosphorus compounds have a 96-hour TL_m as low as 0.2 mg/l (Henderson and Pickering, 1957; Hoffman, 1957).

The development of the organic phosphorus insecticides has had an unusual history in that the mode of action had an early elucidation and has been an extremely fruitful area of investigation for toxicological studies (Metcalf, 1959). The toxic action in insects results from inactivation of the enzyme cholinesterase. This inactivation has been shown to occur in the brain of fish following expo-

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sure to the organic phosphorus compounds (Weiss, 1958, 1959).

In the studies to be reported the degree of inhibition of the brain cholinesterase of several species of fish was examined following *in vivo* exposure to organic phosphorus insecticides. The exposures were made at concentrations that might be expected in aquatic environments following insect control operations.

METHODS AND MATERIALS

Inactivation of cholinesterase in the fish was determined in the fish brain. The brain is essentially nerve tissue and is rich in the true cholinesterases as compared to the pseudo-cholinesterases found in blood (Whittaker, 1951). In most species of fish the brain is readily accessible and is easily removed *in toto*. The brain is supplied with oxygenated blood that comes directly from the gills. The transfer, therefore, of toxic materials from the water across the gill membranes and to the reaction site is quick and direct.

The brain cholinesterase activity is determined using acetylcholine chloride as the substrate. Acetylcholine is the material destroyed *in vivo* by the action of cholinesterase at nerve fiber junctions. A brain homogenate with a tissue concentration of 3-4 mg/l in a phosphate buffer at pH 8.2 is incubated with 0.004 *M* acetylcholine chloride at 25° C. for 20 minutes. The residual acetylcholine is determined colorimetrically by the Hestrin method (Hestrin, 1949). The brain acetylcholinesterase (AChE) activity is reported as micromoles of acetylcholine hydrolyzed per milligram (wet weight) of brain tissue per hour.

To determine the effect of the organic phosphorus insecticides on fish by the interaction with the brain acetylcholinesterase *in vivo*, it is necessary to establish the limits of normal brain enzyme activity of the various fish species that may be encountered or used for experimental purposes. In earlier studies on fish brain cholinesterase, it was found that both variation in activity per unit weight of brain and variation among species were problems that had to be resolved to establish a basis for the use of the brain enzyme activity as a method of detection of organic phosphorus insecticides in water (Weiss, 1959).

Curves of best fit for the array of points for several species of fish (*Micropterus salmoides*, largemouth bass; *Lepomis macrochirus*, bluegill; *Notemigonus crysoleucas*,

golden shiner; *Carassius auratus*, goldfish) indicate a decrease of activity per unit weight as the brain weight increases (Figures 1 and 2). For either experimental material or specimens obtained from natural sources, therefore, the brain weight of individual fish can be used as the reference for determining normal activity of the specimen. This reference assumes nonexposure to contamination that would inhibit brain cholinesterase. The expected limit of normal activity, based upon the variation found in the control specimens represented in the figures, was established. The limits describe the variation to be expected at any particular brain weight. The line of the graph was considered as 100 percent activity and percentages of normal activity were calculated from it. Approximately two-thirds of the brain activities recorded were within the area ranging from 10 percent above to 10 percent below the line of normal activity (one standard deviation).

The data presented in Figures 1 and 2 represent specimens analyzed over a period of time in 1956 and 1957 and were obtained from several sources as indicated. In the course of further studies additional specimens were assayed approximately 1 to 2 years later and the results of these are shown in Figure 3. The distribution of points is similar to that of the earlier figures and the curves of best fit that were determined for the earlier data have been superimposed in this figure. It is evident that the curve of normal activity developed for the earlier material still holds. Within a limited size range of fathead minnow (*Pimephales promelas*) available, the normal brain activity values were determined by calculating the arithmetic mean for several brain size classes.

The organic phosphorus insecticides used in this study were obtained from various sources, either direct from the manufacturer or from technical agencies involved in insecticide investigations. A list of the compounds employed, their common name, and current used chemical name is presented in Table 1. Weighed samples of these compounds were prepared in acetone solution. Acetone, which has negligible toxicity to fish, provided a suitable carrier for introducing these insoluble materials into water. Corrections in concentration were made for the relative degrees of chemical purity reported for the compounds.

Fish were obtained from private, Federal or state hatcheries. Since specimens were generally 3 to 4 inches in length, 14 to

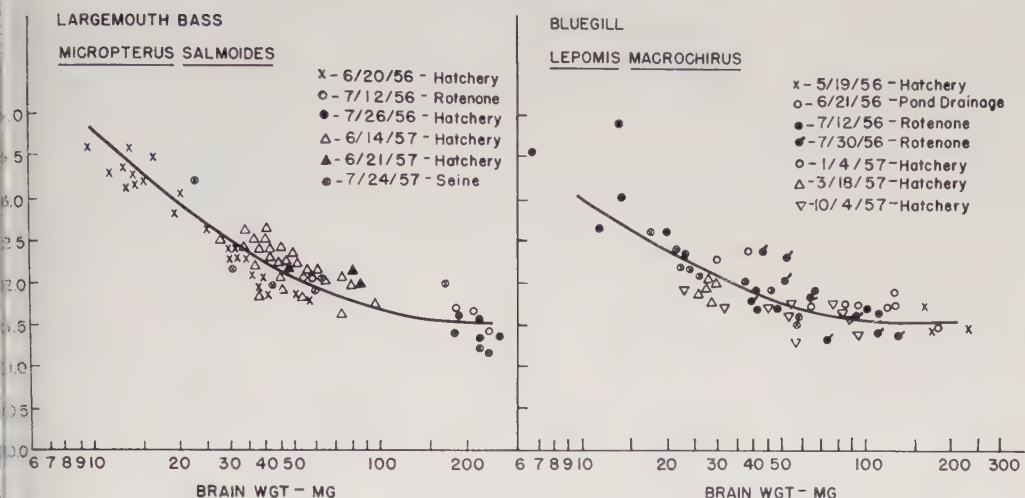


FIGURE 1.—Normal brain acetylcholinesterase activity of the largemouth bass and bluegill as a function of brain weight.

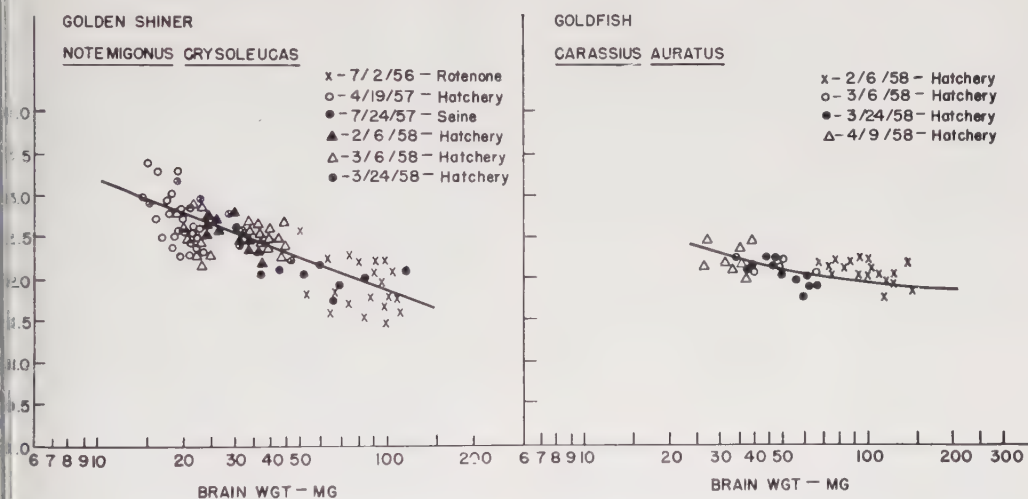


FIGURE 2.—Normal brain acetylcholinesterase activity of the golden shiner and goldfish as a function of brain weight.

specimens could be used in 15 liters of water. Experimental exposures of fish to the test compounds were carried out in 5-gallon wide-mouth jars. Dechlorinated Chapel Hill tap water (a soft surface water) with the pH adjusted to 6.5 to minimize hydrolysis was used. The test vessels were calibrated to 15 liters and appropriate quantities of chemical material were introduced to provide the desired concentrations. When large numbers of fish had to be exposed to provide specimens for long-term survival, duplicate sets at similar concentrations were simultaneously ex-

posed. All exposures were made at 20–21° C., and the water was saturated with the air gases prior to the start of an experiment. Following exposures, test specimens were frozen until assayed. At –25° C. or lower there is no significant change in brain enzyme activity of frozen fish for as long as 3 months' storage.

RESULTS

The problem of comparing species reaction to the organic phosphorus insecticides and the relative change in brain enzyme activity at the point of death was examined by expos-

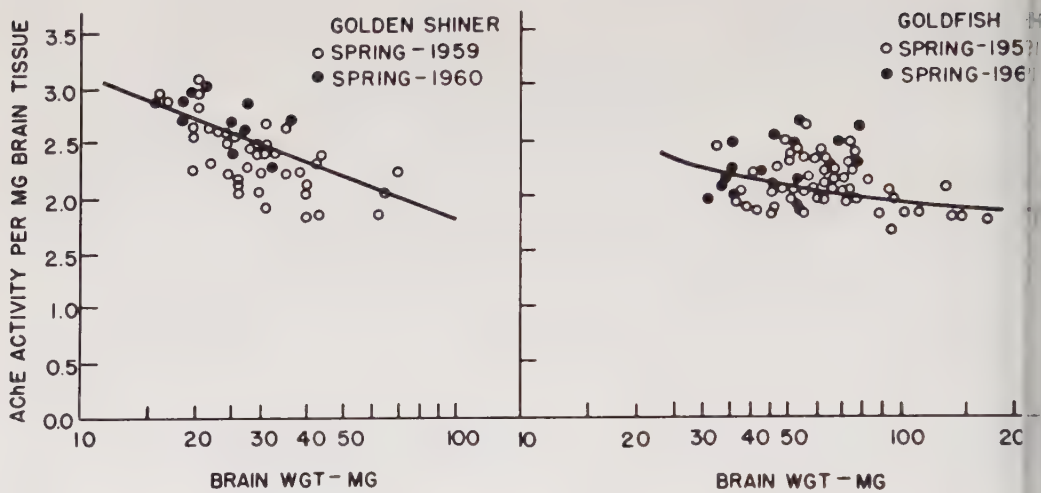


FIGURE 3.—Normal brain acetylcholinesterase activity of the golden shiner and goldfish. A comparison of the curve of normal activity previously determined with data of 1959 and 1960.

ing largemouth bass and fathead minnows to 10 different formulations. The insecticide concentrations were the same for each species. The time of termination was at the exposure resulting in approximately one-half of the dead fish or the LT_{50} . The brain AChE activity of the sets of dead and live specimens was then determined. Each value shown in Table 2 represents an average of approximately six brain analyses.

On exposure to 0.5 mg/l of the various compounds, these two species of fish demon-

strated considerably different degrees of sponse. In less than 1 hour the survival largemouth bass exposed to Guthion. Diazinon had brain AChE activity reduced less than 6 and 18 percent of normal, respectively. The next compound to produce least effects was malathion after 2 hours and minutes' exposure, when brain enzyme activity was reduced to less than 24 percent normal. After 9½ hours the largemouth responded to EPN, but the fish alive at time had brain enzyme activity of about percent of normal, whereas those dead brain enzyme activity averaging about percent of normal. After exposure of hours no further deaths had occurred and the largemouth bass subjected to the formulations.

At 12 hours fish sampled from the exposure vessels containing parathion, Di-Syston, VP, and Co-Ral had brain enzyme activity of less than 30 percent of normal for the three and about 45 percent of normal for Co-Ral. At the end of 24 hours dead specimens were found in the parathion and Syston exposures with brain activities about 24 percent of normal for the parathion and about 15 percent for the Di-Syston. Fish sampled from DDVP had just under 30 percent of normal brain enzyme activity at time, but no deaths had occurred. Similar in the Co-Ral exposures brain activity reduced to about 45 percent with no deaths. Continued exposure of the survivors to Co-Ral resulted in deaths in 36 hours with h

TABLE 1.—Chemical and common names of organic phosphorus insecticides

Common or trade name	Compound ¹
Parathion	O, O-diethyl O- <i>p</i> -nitrophenyl phosphorothionate
Chlorthion	O, O-dimethyl O-(3-chloro-4-nitrophenyl) phosphorothionate
Diazinon	O, O-diethyl O-(2-isopropyl-4-methyl-6-pyrimidyl) phosphorothionate
Co-Ral	O, O-diethyl O-(3-chloro-4-methylumbelliferone) phosphorothionate
Malathion	O, O-dimethyl S-(1, 2-dicarboethoxyethyl) phosphorodithionate
Guthion	O, O-dimethyl S-(1, 2,3-benzotriazinyl-4-keto)-3-methyl phosphorodithionate
EPN	O-ethyl O- <i>p</i> -nitrophenyl phenylphosphonothionate
DDVP	O, O-dimethyl O-2, 2-dichlorovinyl phosphate
Demeton	O, O-diethyl O-(and S-)-ethyl-2-thioethyl phosphorothioates
Di-Syston	O, O-diethyl S-ethyl-2-thioethyl phosphorodithioate
Delnav	2, 3- <i>p</i> -dioxanedithiol S, S-bis-(O, O-diethylphosphorodithioate)
Dipterex	O, O-dimethyl 1-hydroxy-2, 2, 2-trichloroethylphosphonate

¹ Metcalf (1959)

TABLE 2.—The percentage of normal AChE activity at the approximate LT_{50} and at total exposure in largemouth bass and fathead minnows

[Insecticides listed in approximate order of toxic effectiveness at 0.5 mg/l]

Insecticide	Largemouth bass			Fathead minnow		
	Time	Live	Dead	Time	Live	Dead
Guthion	40 min.*	5.4	3.8	40 min.*	51.5	44.9
Diazinon	1 hr.*	17.5	28.1	80 min.*	29.1	38.2
Malathion	2 hr. 40 min.*	23.9	17.1	24 hr.	70.8	69.7
EPN	9 hr. 30 min.*	41.9	60.2	72 hr.	51.1	None
Parathion	24 hr.*	24.3	23.5	1 hr. 15 min.*	92.0	98.6
Di-Syston	24 hr.*	16.7	13.7	24 hr.	81.5	66.3
Co-Ral	36 hr.*	24.0	31.1	72 hr.	42.2	None
DDVP	48 hr.*	23.5	18.8	24 hr.	45.2	None
Delnav	—	—	—	72 hr.	37.7	None
Demeton	—	—	—	24 hr.	—	—
Chlorthion	—	—	—	72 hr.	77.8	None
				24 hr.	49.8	None
				72 hr.	45.5	None
				24 hr.	58.3	None
				72 hr.	42.5	None
				24 hr.	68.5	None
				72 hr.	53.6	None
				24 hr.	87.5	None
				72 hr.	76.7	None

*At these exposure times one-half the exposed fish had succumbed.

activity reduced to about 30 percent of normal.

After 48 hours death had occurred in DDVP exposures with brain activity reduced to less than 25 percent of normal.

In the parallel set of exposures with fathead minnows, the response was quite different in several respects. In less than an hour LT_{50} was reached in the Guthion exposure, with brain activities of 50 percent of normal in the living specimens and about 45 percent in the dead specimens. In 75 minutes the LT_{50} was reached in the EPN exposures, but brain enzyme activity showed no appreciable reduction below the normal range. A minutes later the fish exposed to Diazinon reached the LT_{50} with brain activity in living fish of about 29 percent of normal and in the dead specimens, 38 percent of normal.

Other compounds produced lethal reactions through the twelfth hour of exposure. At that time, among the living specimens sampled, malathion produced the largest brain activity reductions to just under 60 percent; the remainder ranged upward to within normal range of brain enzyme activity for the fish exposed to DDVP, Chlorthion, Delnav, demeton, and Co-Ral. At 24 hours lethal response was found in the exposures to malathion, parathion, and Chlorthion with brain activity reduced from normal in both living and dead specimens to approximately 70 percent for malathion, 81 percent in the living and 66 percent in the dead for parathion, and

about 87 percent for the living and 85 percent in the dead fish exposed to Chlorthion. The other compounds all showed somewhat greater reductions of brain enzyme activity with no deaths ensuing. The fish exposed to Di-Syston had brain enzyme activities as low as 45 percent of normal. Continued exposure in the seven compounds for as long as 72 hours showed no further mortalities. Brain enzyme activity continued to be reduced and fell as low as 38 percent of normal for Di-Syston. After 72 hours' exposure, however, Co-Ral had produced a reduction in brain activity to only 78 percent of normal.

The non-reactivity of the fathead minnow to these compounds is in marked contrast to the largemouth bass which showed a greater degree of enzyme inactivation and mortalities in shorter periods of exposure. Part of the slowing of the reaction to the organic phosphorus compounds in the 72 hours of exposure may be due to hydrolysis of the molecule.

It is worth noting that when brain enzyme activity was markedly reduced from prior exposure, the sensitivity to subsequent exposure to fresh test chemicals was considerably increased, as previously demonstrated with fathead minnows and compounds analogous to the organic phosphorus insecticides (Weiss, 1958).

The relative instability of the organic phosphorus insecticides in water generally implies a reduction in toxicity. The products of hydrolysis are thus less toxic than the original

TABLE 3.—Effect of pH on the *in vivo* inhibition of fish brain acetylcholinesterase in goldfish and golden shiner, expressed as percentage of normal brain AChE activity

[(D)—dead on sampling; (L)—live on sampling]

Exposure (hours)	Dipterex 1.0 mg/l				DDVP 1.0 mg/l	
	Goldfish		Golden shiner		Golden shiner	
	pH 6.5	pH 8.0	pH 6.5	pH 8.0	pH 6.5	pH 8.0
1	114	101	—	—	—	—
2	109	99	71	89	72	79
4	102	98	69	85	70	70
6	104	85	79	68 (D) 72 (L)	63	50 (D) 59 (L)
12	93	82	51	—	61	—
24	—	—	—	—	53	—

compound. Two of the compounds in general use, Dipterex and DDVP, on hydrolysis have been recorded, however, as producing materials of increased toxicity (Metcalf, 1959). An experiment was carried out to test this chemical behavior and ascertain the effect on the brain AChE activity of the fish used in this study. Since these compounds are comparatively non-toxic under normal circumstances, a relatively high concentration of 1.0 mg/l was employed.

As shown in Table 3, during the course of exposure to both Dipterex and DDVP, the decrease in the percentage of normal AChE activity was greater under alkaline conditions. After 12 hours' exposure to Dipterex the goldfish exhibited a relatively small but consistently greater inhibition of brain enzyme activity at pH 8.0. In contrast, the golden shiner showed a greater degree of response. At pH 6.5, the 12-hour exposure produced a marked decrease of brain enzyme activity but not to the point where death had occurred. At pH 8.0 at the end of 6 hours, approximately one-half of the fish exposed were dead with brain AChE of 68 percent of normal, and the remainder were living with 72 percent of normal activity. On exposure to DDVP at pH 6.5 the shiners again showed a marked reduction of brain enzyme activity, reaching as low as 53 percent after 24 hours. At the end of 6 hours at pH 8.0, however, approximately one-half had died with brain enzyme activity 50 percent of normal, whereas those living had approximately 59 percent of normal activity.

The response of fish to organic phosphorus insecticides can also be examined in the period following exposure during the course of recovery. In many instances the rate of recovery to normal is a reflection not only of

species differences but also of the chemical formulation. In a series of exposure-and-recovery sequences four species of fish, the bluegill, goldfish, golden shiner, and fathead minnow, were exposed to five insecticides. The bluegill and fathead minnow to five additional formulations. All exposures were at 1.0 mg/l except for Guthion in which the exposures were made at 0.01 mg/l. The low concentration of Guthion was established in order to maintain approximately the same scale of reaction time as with the other compounds. The exposure periods at 20° C. were usually terminated at 12 hours except for the fathead minnow which was generally exposed for a total of 24 hours. Shorter exposure periods of 6–7 hours were used in some instances for the bluegill, and the exposure was terminated when outward symptoms (pectoral fins held in a rigid forward position, for example) indicated approaching lethality. The results of these exposures and recovery series are shown in Figures 4 to 8. Except in Figure 8 the chemicals paired in each figure have similar basic chemical structures (Table 1).

The reaction to and recovery from exposure to organic phosphorus insecticides varies considerably for each fish species. Undoubtedly the bluegill responds faster and recovers more slowly than the other species. Where comparison between all four species is possible, the goldfish, although responding more rapidly than the minnow and golden shiner as indicated by degree of brain enzyme inactivation, also recovers faster. This pattern is particularly evident in the parathion, Delnav, and DDVP exposures.

As shown in Figure 4 the exposure period to Chlorthion results in minimal brain enzyme inactivation. After removal from exposure tanks, however, the fathead minnow showed brain enzyme inactivation down to 20 percent of normal after 6 days followed by recovery to normal in about another 6 days. The comparison exposure of bluegills indicated inactivation persisting for more than 40 days with no indications of recovery to normal.

Parathion exposures produced, on the other hand, marked brain inactivation followed by a prolonged and a consistently rising trend toward recovery which probably requires more than 60 days. Death of the exposed fathead minnows prior to full recovery may have been due to secondary effects. It has also been observed with fish exposures to parathion

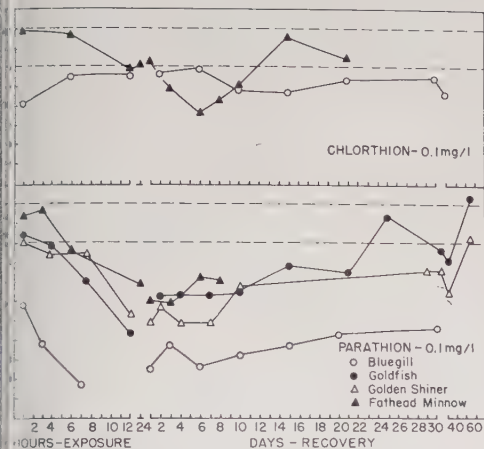


FIGURE 4.—The change in fish brain acetylcholinesterase activity on exposure to Chlorthion and parathion and in the subsequent recovery period.

brain enzyme recovery tends to lag for several days before the upward trend is definitely established.

The reaction of fish exposed to Co-Ral and diazinon, compounds similar in basic chemical structure to Chlorthion and parathion and also being phosphorothionates, showed parallel features. From Figure 5 it was evident that following exposure to Co-Ral both bluegill and fathead minnow exhibited a continued low level of brain enzyme activity the first 10 days of the recovery sequence and had not attained full recovery by the end of 30 days.

The effectiveness of Diazinon in inhibiting brain enzyme activity was seen in the response of the bluegill and fathead minnow requiring only 6 hours to bring the former down to less than 10 percent of normal and the latter in 12 hours to less than 30 percent of normal. In the goldfish and golden shiner had lesser degrees of brain enzyme inhibition in 12 hours, or about 60 percent of normal. Recovery in nearly all instances appeared to be immediate and rapid with the duration depending on the extent of initial inhibition.

Guthion and malathion, although both are phosphorodithionates with a basic chemical similarity, showed considerable difference in their relative toxicity. In order to produce the same approximate order of brain enzyme inhibition on the same time scale, Guthion had to be used at 0.01 mg/l as compared to malathion and other compound dosages of 0.1 mg/l. Even with this change the reaction of Guthion was in some instances consider-

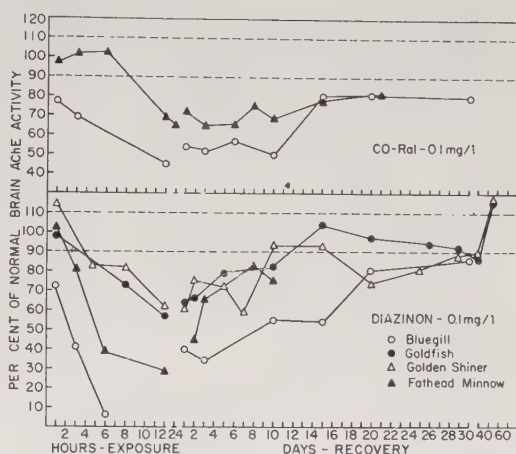


FIGURE 5.—The change in fish brain acetylcholinesterase activity on exposure to Co-Ral and Diazinon and in the subsequent recovery period.

ably more severe at equivalent times of exposure. For example, the fathead minnow had 42 percent of normal brain activity in 24 hours' exposure to Guthion but 80 percent on exposure to malathion at 10 times the dosage. In the latter case, however, brain activity dropped to 62 percent of normal on the third day before recovery started.

As shown in Figure 6 the rapid rise in brain activity in the first 24 hours of recovery, followed by a much slower rate of recovery before the normal range of activity was attained, is a characteristic pattern. Except for the fathead minnows exposed to

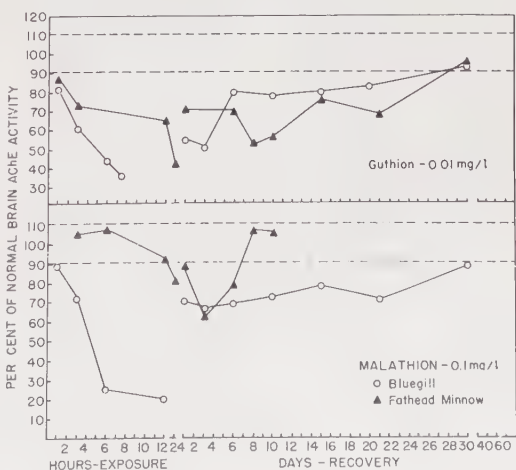


FIGURE 6.—The change in fish brain acetylcholinesterase activity on exposure to Guthion and malathion and in the subsequent recovery period.

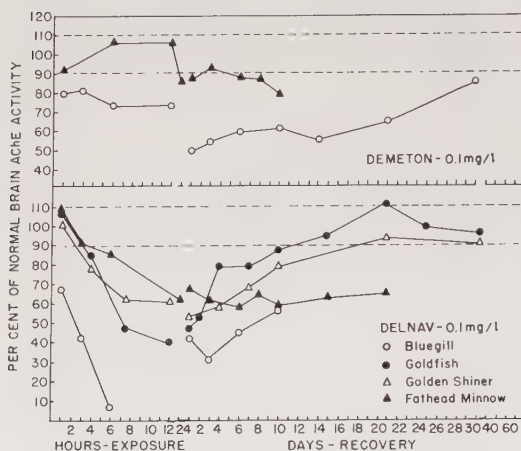


FIGURE 7.—The change in fish brain acetylcholinesterase activity on exposure to demeton and Delnav and in the subsequent recovery period.

malathion the pattern was fairly consistent. This prolonged recovery suggests continued inhibition or irreversible inhibition of cholinesterase. Until new enzyme is produced the total brain enzyme activity shows varying degrees of less than normal activity.

The brain enzyme activity of fish exposed to demeton and Delnav, shown in Figure 7, again highlights both chemical and biological species differences. On exposure to demeton the extent of inhibition of the brain activity of the fathead was minimal even after 24 hours. In the subsequent recovery period, however, a trend toward further brain inactivation was established and fell below 80 percent of normal by the 10th day. On the other hand the bluegill showed brain inactivation to 70 percent of normal in 12 hours' exposure, but in the first 24 hours of recovery brain activity had dropped to 50 percent of normal. A prolonged period of low brain enzyme activity, which lasted nearly 2 weeks, followed before a clear upward trend was established.

In comparison the fish exposed to Delnav either showed little change from the 12- or 24-hour exposed condition in the first 24 hours of recovery or, in the case of the bluegill, a rapid rise. The goldfish and golden shiner both recovered to normal ranges of activity in about 2 and 3 weeks, respectively. In contrast, the fathead minnow exhibited a prolonged and consistent level of brain activity in the 60 to 70 percent of normal range through the 21 days that determinations were carried out. Bluegill material was not avail-

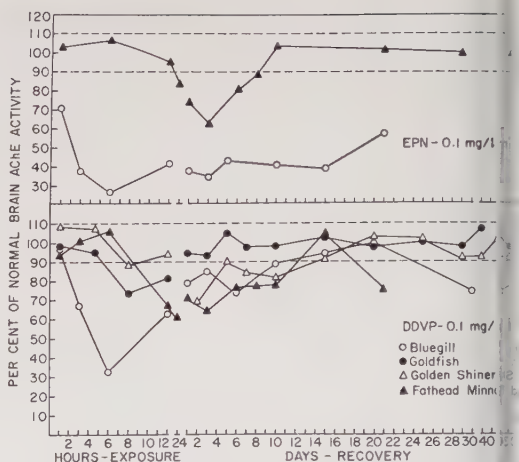


FIGURE 8.—The change in fish brain acetylcholinesterase activity on exposure to EPN and DDVP and in the subsequent recovery period.

able after 10 days' recovery but the established trend might indicate recovery to normal in 3 to 4 weeks.

The two compounds EPN and DDVP provide further contrasts in reactivity of the various fish species to the organic phosphorus insecticides. As shown in Figure 8 the brain enzyme reaction to EPN illustrates the phenomena of little inactivation in the fathead minnow during the exposure period, followed by further inactivation in the initial recovery sequence and then rapid recovery to normal in about 10 days. The fathead minnow has shown similar exposure-recovery curves with Chlorthion and malathion. The bluegill contrast showed considerable brain enzyme inhibition in the exposure period followed by more than 2 weeks of continued low brain activity around 40 percent of normal before a trend toward normal was established.

Exposures of the four fish species to DDVP showed the greater sensitivity of the bluegill but also a generally rapid recovery to normal. The goldfish attained the normal range within the first 24 hours of recovery and remained there. The golden shiner, fathead minnow and bluegill required somewhat more than 24 days to attain normality.

DISCUSSION

In the preceding analysis of the response of fish brain cholinesterase exposed *in vivo* to organic phosphorus insecticides and the response of the enzyme subsequent to exposure, distinct patterns characteristic of the fish and

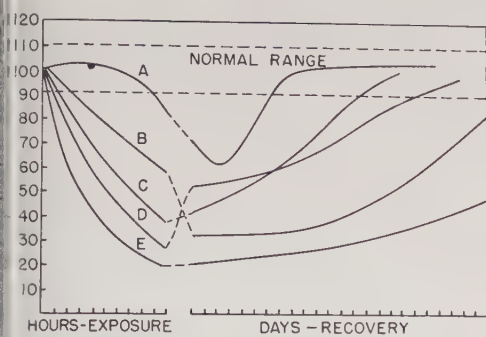


FIGURE 9.—Five types of generalized exposure-recovery curves described by the degree of brain cholinesterase inactivation of fish species exposed to organic phosphorus insecticides.

tical species have been indicated. The patterns of reaction and recovery experimentally described in Figures 4 to 8 may be generalized as shown in Figure 9. Curve A illustrates little or no brain enzyme inhibition during the exposure period, a continued fall in the initial recovery period with quick attainment of the low value, and then rapid recovery. Curve B describes a moderate inhibition during the exposure period, a sharp further drop during the first 24 hours of recovery, and a prolonged lag in the recovery period before a return of recovery to normal is established. Curve C shows that there is little or no change between the end of exposure and the first day of recovery and that the return to normal proceeds more or less systematically with no lag. Curve D shows a sharp rise in brain enzyme activity in the first 24 hours of recovery followed by a lag of several days before there is a more systematic rise to the normal range. Curve E generally illustrates a marked and prolonged inhibition with a considerable lag in the initial recovery sequence before an upward trend is distinctly established.

Using these five generalized curves of exposure and recovery the interaction between fish brain cholinesterase and organic phosphorus insecticides may be summarized (Table 4).

The formation of impurities by side reactions during synthesis or by rearrangement and storage (Metcalf, 1959) makes it particularly questionable to make categorical statements concerning the toxic reactions of the organic phosphorus insecticides, but it is evident from the preceding summary of exposure-reaction curves that a pattern of relationships exists between the species and in the compounds. The bluegill appeared to respond

TABLE 4.—Exposure-recovery curve types¹ for four fish species and several organic phosphorus insecticides

Insecticide	Bluegill	Goldfish	Golden shiner	Fathead minnow
Parathion	E	D	E	E
Chlorthion	E	—	—	A
Diazinon	D	C	C	D
Co-Ral	E	—	—	E
Malathion	D	—	—	A
Guthion	D	—	—	E
Delnav	D-C	C	C	E
Demeton	B	—	—	A-E
DDVP	D	D	B	C
EPN	E	—	—	A

¹ Letters designate curve types as shown in Figure 9.

to all the compounds with a rapid brain enzyme inactivation followed in the recovery sequence by a period of little or no recovery. The capacity of this species for detoxification or destruction of residual insecticide by phosphatases appeared to be minimal. In contrast the fathead minnow showed, particularly with Chlorthion, malathion, and EPN, a considerable resistance to brain enzyme inactivation plus a capacity for rapid detoxification or recovery.

Where a curve type is described by two letters it is indicative of the characteristic of the first on exposure and the second on recovery. Thus on exposure to Delnav, although the bluegill inactivation was rapid and severe, there followed a sharp rise in the first 24 hours of recovery rather than a lag. The recovery curve then proceeded to rise rapidly. It is of interest to note that with Delnav both the goldfish and shiner also had C-type curves but the fathead minnow curve was a distinct E type.

These characteristic toxic response patterns indicate that considerable physiological variation can be expected among fish species. Variations in sensitivity or tolerance to other toxic compounds are probably due to similar biochemical processes of enzyme inactivation and detoxification as has been indicated here for the organic phosphorus insecticides.

The ability to detect the inhibition of fish brain cholinesterase subsequent to the actual exposure for 1 to 3 weeks or longer provides a unique technique for demonstrating prior exposure to organic phosphorus insecticides in the aquatic environment.

CONCLUSIONS

Fish exposed to low concentrations, 0.1 mg/l, of organic phosphorus insecticides show

inhibition of brain acetylcholinesterase. The degree of reaction to the cholinesterase-inhibiting insecticides is not only a function of time and concentration but also of chemical and biological species. Following exposure to the brain-cholinesterase-inhibiting materials the fish demonstrate a capacity for regeneration to normal brain enzyme activity. The necessary regeneration period may be as long as 30 days or more. The assessment of the degree of inhibition of fish brain acetylcholinesterase permits detection of both current and past contamination of water by organic phosphorus insecticides.

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Environmental Changes in Lake Erie¹

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ABSTRACT

Comparison of data compiled during the past 60 years with those from recent studies shows that major changes have occurred in the bottom and fish faunas of Lake Erie. The bottom fauna was formerly dominated by the nymphs of *Hexagenia*, but at present midge larvae and oligochaetes are most abundant. Blue pike (*Stizostedion vitreum glaucum*) and cisco (*Coregonus artedii*), which formerly dominated the commercial catch, are scarce, while other species are more plentiful than formerly. The concentrations of various major ions have increased as much as 10 p.p.m. The mean annual water temperatures are approximately 2° F. warmer today than during the 1918-28 period. Low levels of dissolved oxygen have been observed several times since 1930, and recently very low concentrations were found in the bottom waters covering many square miles of the central basin. Although similar conditions may have existed in the past, it appears that greater areas are involved at the present.

INTRODUCTION

It has been stated that Lake Erie has changed during the past 60 to 100 years and these changes may be due to rising intrusions of sewage and other materials from increased human population (Powers, 1959; Mundinger, and Ayers, 1959). It has been suggested that the lake is undergoing accelerated eutrophication (Beeton, 1959). Heretofore no attempt has been made, however, to make a detailed examination of the available data that might show such changes in the lake.

A marked change in Lake Erie would offer a unique situation since eutrophication has not been demonstrated in a lake of this size. Studies have been made of the eutrophication of a number of lakes (Hasler, 1947). Probably the best documented is that of the Zurichsee, Switzerland, where the deeper basin, previously changed in a relatively short time from an oligotrophic to a eutrophic condition (Mander, 1926). Evidence of eutrophication in Lake Washington has recently been published (Edmondson, Anderson, and Peterson, 1959).

Lake Erie is the shallowest of the five Great Lakes, with a mean depth of 63.9 feet (Wright, 1955). It is naturally divided into three commonly recognized sections by two prominent peninsulas, Point Pelee and Long Point (Figure 1). The eastern basin, east of the connecting Erie, Pennsylvania, and the western basin, west of Long Point, is the deepest portion of the lake (maximum depth, 210 feet). The

central basin, between Long Point and Point Pelee, makes up the greater portion of the lake. It has a very uniform bottom, and most of its area is between depths of 60 and 78 feet. The area west of a line connecting Sandusky, Ohio, and Point Pelee is the shallow western basin (maximum depth, 54 feet).

Several studies have been made of Lake Erie during the past 60 years. The U. S. Geological Survey made chemical analyses of Great Lakes waters in 1906-07 (Dole, 1909). A survey was made of coliform bacteria in Lake Erie in 1913 (International Joint Commission, 1914). Many of these sampling stations were revisited in 1946-48 (International Joint Commission, 1951). The Bureau of Fisheries took part in two co-operative surveys: western basin, 1928-30 (Wright, 1955), and central and eastern basins, 1928-29 (Fish, 1960). Chandler (1940, 1942a, 1942b, 1944) and Chandler and Weeks (1945) made extensive collections of plankton and physical-chemical data in the Bass Island region, 1938-42. The Fisheries Research Laboratory, University of Western Ontario, conducted limnological investigations in the central basin, 1947-53 (Powers *et al.*, 1959). The Bureau of Commercial Fisheries has been collecting extensive limnological information since 1957. These studies of open-lake conditions can be supplemented by water-quality data collected at various water-treatment plants. It has been demonstrated that the intakes of several of these plants (Lorain, Ohio; Cleveland, Ohio; Erie, Pennsylvania; and Woodlawn, New York) are situated so that open-lake water is taken in rather than littoral waters which are frequently influenced by local river discharge. Consequently, data

¹Presented at the meeting of the Lake Erie Fish Management Committee, Niagara Falls, Ontario, May 1960.

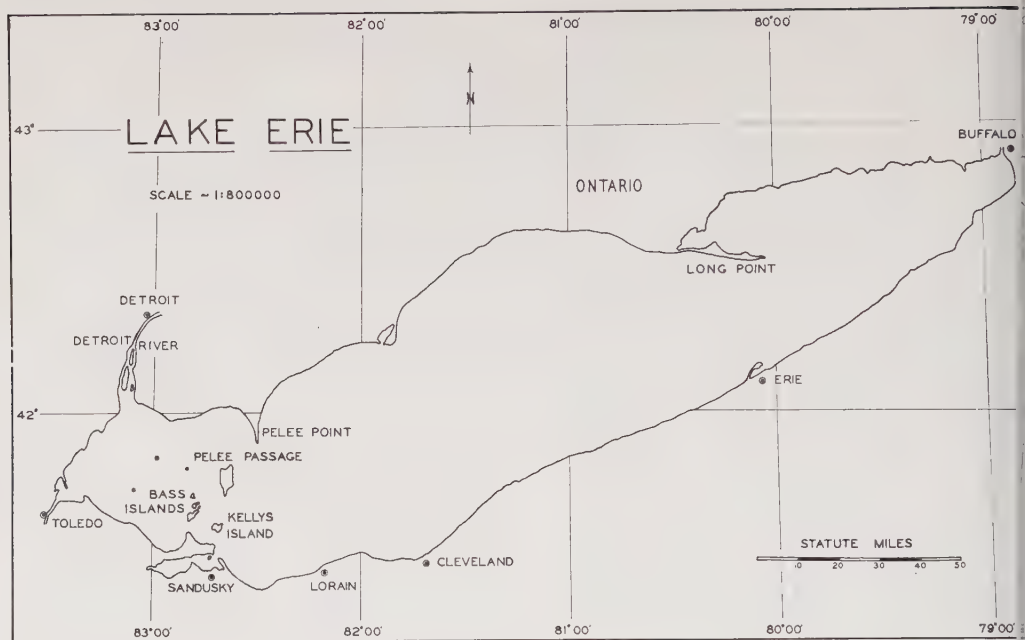


FIGURE 1.—Lake Erie.

from these sources represent open-lake conditions (Powers *et al.*, 1959).

BIOLOGICAL DATA

The present study does not concern itself with changes in the fish population, although some of these changes are no doubt related to progressive modifications of the environment. Shifts involving regularly exploited species, such as the collapse of the cisco (*Coregonus artedii*) fishery in the middle 1920's, the long-term upward trend of the walleye (*Stizostedion vitreum vitreum*) from the early 1930's to the middle 1950's, and the recent near-disappearance of blue pike (*Stizostedion vitreum glaucum*) and sauger (*Stizostedion canadense*), have been well documented in published statistics and some have been discussed in special articles. We have only limited knowledge, however, of the extent of increase of such little-utilized species as gizzard shad (*Dorosoma cepedianum*) and alewife (*Alosa pseudoharengus*) or of the American smelt (*Osmerus mordax*), which is exploited commercially in Canada only.

Bottom fauna

Evidence is convincing that major changes have occurred in the bottom fauna. Prior to

1953 the population of mayfly larvae (*Plecoptera*) in the island region was around 44 per square meter of lake bottom (Britt, 1955a). A prolonged period of calm weather in the summer of 1953 resulted in the stratification that was accompanied by severe oxygen depletion in the bottom waters. One week later Britt (1955a) found only 44 mayfly larvae per square meter. The population recovered rapidly in 1954 (Britt, 1955b). In 1957 we found only 39 nymphs per square meter.

Preliminary analysis of our data from 1957 shows that the number of stations around the islands where oligochaetes increased from 12 per square meter in 1929 (Wright, 1955) to 55 per square meter in 1957 and midge larvae from 56 per square meter in 1929 to 299 per square meter in 1957. Caddisfly larvae were formerly abundant but averaged less than 1 per square meter in 1957. The nature of these changes is well illustrated in the comparison of data collected by the same methods in similar sediments and depths from stations on South Bass Island in 1929-30 and in 1957 (Table 1). Similar changes were observed in Maumee Bay by Brown (1953) when he compared his 1951 data with those published by Wright (1955).

TABLE 1.—Number of bottom organisms per square meter in the vicinity of South Bass Island in 1929–1958 (Wright, 1955) and in 1958

Item	1929 Station 158	1930 Station 158	1958 Station 2	1958 Station 3
Number of samples	20	16	40	7
Hydra	6	4	37	27
Chaetetes	6	3	559	635
Hydra	312	515	49	44
Hydridae	81	22	257	280
Hydras	12	24	7	0
Small clams	16	8	55	37
Hydras	20	1	3	0

limited data from the area 4 miles east of South Bass Island, which may be representative of the central basin for 1929, 1930, 1957, and 1958. These data show that the large larvae of the midge, *Chironomus tentans plumosus*, have replaced the midges as the dominant larger organisms. *Oligochaetes* and fingernail clams showed an increase over the 1929–30 samples. A comparison of the 1957 samples with those of 1929–30 after a period of very low oxygen values in the central basin in 1959 showed that numbers of all organisms except nematodes had increased.

Bacteria

The bacterial load at the outlet of the Detroit River increased threefold between 1941 and 1946–48 (International Joint Commission, 1951). Similar increases were found in the entire western basin. In 1913 the average concentration of coliform bacteria was 2 per 100 milliliters; in 1946–48 it was 20 per 100 milliliters.² This increased bacterial load is related to a population growth in the area from about 1,000,000 in 1910 to 10,000,000 in 1948. The counts did not change significantly between 1913 and 1946–48 in western Lake Erie: “. . . the bacterial pollution of the main body of eastern Lake Erie is the same as in 1913” (International Joint Commission, 1951, p. 290).

Plankton

Information on the plankton is insufficient for a valid comparison of earlier and more recent years.

The average for 1913 based on data from stations 109 and 274–285 (International Joint Commission, 1914). The 1946–48 average is based on data from table 22, sampling ranges B-H-R-C, A-G, G-N, W-F, G-F, T-N, R-F, C-K-E, F-E, E-M, and (International Joint Commission, 1951). The results, expressed in terms of the Phelps Index, multiplied by 2.4, as suggested by the International Joint Commission (page 70, 1951), to make comparisons between the two investigations.

Furthermore, the studies that have been made show great seasonal fluctuations and considerable year-to-year differences in abundance. The statement made by Chandler and Weeks (1945) that, “Until a greater knowledge of the extent of the annual variations is acquired any attempt to generalize on the basis of observations limited to one season or even a complete year will have little meaning,” is still valid, especially since the plankton of Lake Erie has received little attention in the last 15 years. Chandler (1942b) found that the composition and abundance of plankton in the island region in 1939 was closely similar to that of 1929–30 (Wright and Tidd, 1933). Despite sharp differences between Chandler’s 1939 and 1940 samples, the relative importance of diatoms and green and blue-green algae was approximately the same in 1929–30 and 1939–40.

PHYSICAL AND CHEMICAL DATA

Temperature

Water temperature records from the Chestnut Street filtration plant at Erie, Pennsylvania, show a definite increase in mean annual values for the 1918–58 period (Erie, Pennsylvania, Bureau of Water, 1958). The moving means of these temperatures indicate that the lake is between 1.5° and 2.0° F. warmer than during the 1918–27 period (Figure 2). Moving means were calculated by using the first 10 years as a base (1918–1927); then the eleventh year was added and the first year subtracted to obtain a new average and the process continued through 1958. The moving means are credited to the final year in each decade. A comparison of the moving means of water temperature with 10-year moving means of annual air temperature in southwestern Ontario (Thomas, 1957) shows, as would be expected, that the warming trend of the lake follows that of the climate. The greatest increase in mean annual water temperatures occurred between 1925 and 1930. There has not been a significant change in the trend in the temperature since this warming period.

Transparency

The usual decrease of transparency in a lake undergoing eutrophication has not occurred in Lake Erie. Most of the Secchi-disc readings in the summer of 1929–30 were 1 to 2 meters in the western basin (Wright, 1955). The average disc depth in the summer was

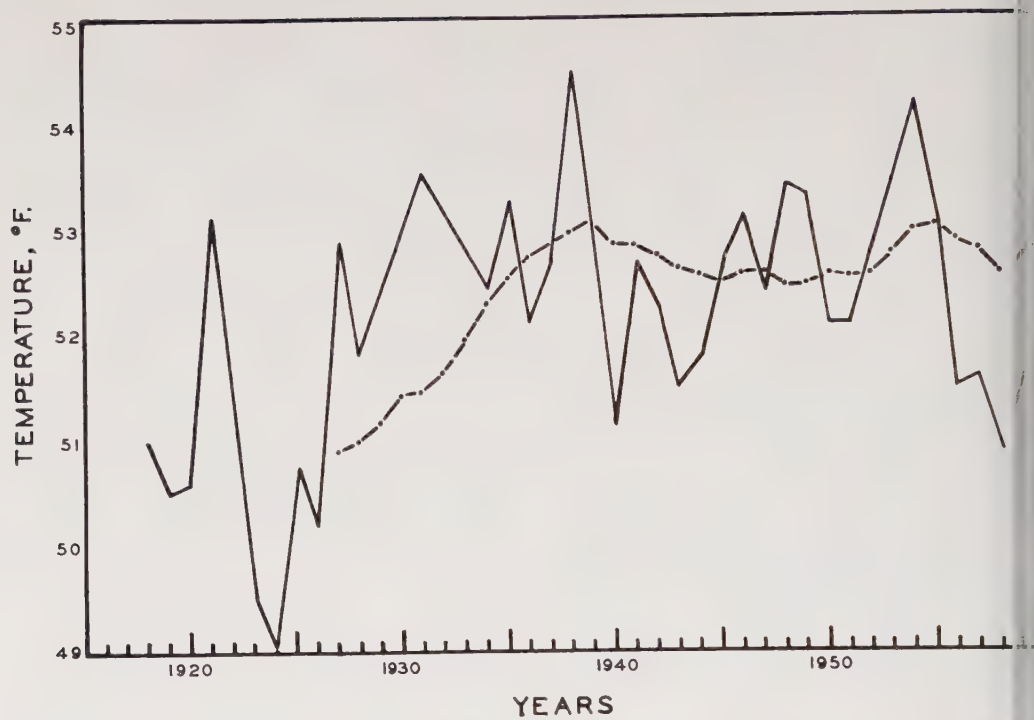


FIGURE 2.—Water temperatures at Chestnut Street filtration plant, Erie, Pennsylvania, 1918–58. Solid line, annual temperature; broken line, 10-year moving means of annual temperature.

1.1 meters in 1939, 1.1 meters in 1940, and 1.7 meters in 1941 (Chandler, 1940, 1942a, 1944). Our average disc depth in the summer of 1958 was 1.5 meters. Similar comparisons can be made for the central basin. The average disc depth in 1929 (Fish, 1960) was 4.0 meters; our average disc reading was 3.3 meters in 1958. Transparency measurements made by the University of Western Ontario (Powers *et al.*, 1959) were all appreciably greater than those recorded elsewhere. Average Secchi-disc depths ranged from 6.4 meters in 1947 to 9.8 meters in 1949 at their station 2. This greater transparency along the north shore of the central basin probably is due to the clearer waters originating from the Detroit River. Our drift-bottle studies of 1958 indicate that the main flow of Detroit River water is through Pelee Passage and along the north shore.

Major ions

The concentrations of most major ions have increased since 1906–07 (Dole, 1909). The recent analyses show increases of from 1 to 10 p.p.m. in calcium, magnesium, sodium plus potassium, and sulfates over the earlier values (Table 2). Total solids increased from

133 to 183 p.p.m. Some earlier determinations of total solids in 1901–03 off Erie, Pennsylvania, averaged 143.5 p.p.m. (Lewis, 1942). Chlorides, recorded by a number of agencies, show a consistent increase. An average of Wright's (1955) data for the island region in 1930 was 10.3 p.p.m. The International Commission average for the western limit

TABLE 2.—Average concentrations (p.p.m.) of major ions and total solids in Lake Erie water

Item	1906–07 ¹	1934–38 ²	1948–49 ³	1957 ⁴	1958 ⁵
Calcium	31.0	38.1	35.7	40.0	36.0
Magnesium	7.6	8.9	8.6	—	8.9
Sodium and potassium	6.5	7.7	9.7	9.9	8.7
Silica	5.9	6.0	2.0	0.9	1.5
Sulfates	13.0	22.1	22.5	20.5	23.0
Chlorides	8.7	14.8	18.2	—	26.0
Total solids	133.0	164.9	168.0	—	183.0

¹ Dole (1909), average of monthly determination September 19, 1906, to August 28, 1907, Buffalo, water intake.
² Leverin (1947), average of six determinations by August 20, 1934, and December 21, 1938, Fort Ont., water intake.
³ Thomas (1954), average of monthly determination February 16, 1948, to February 7, 1949, Chippawa water intake on Niagara River.
⁴ Bureau of Commercial Fisheries data, central basin.
⁵ Erie, Pennsylvania, Bureau of Water, 1958.
⁶ Bureau of Commercial Fisheries data, western limit.

18.7 p.p.m. in 1946-48.³ Our analyses averaged 20.0 p.p.m. in 1958. The increase has been greater in the central and eastern basins. Chlorides averaged 6.4 in 1901-03 (Lewis, 1906), 8.7 in 1906-07 (Dole, 1909), 11.9 p.p.m. in 1929 (Fish, 1960). They increased to 22.2 p.p.m. by 1946-48⁴ and averaged from 20 to 26 p.p.m. in 1956-58 (Erie, Pennsylvania, Bureau of Water, 1956, 1957, 1958). The average concentration was 26.3 p.p.m. at the Buffalo, New York, water intake in 1958 (Public Health Service, 1958).

The concentrations of several ions show definite increases during the 30-year period between 1906-07 and 1934-38 (Table 2). These increases may be related to an increasing population. It was during this period that major population growth occurred in the Lake Erie region. Concentrations of total solids increased steadily at an average rate of about 1 p.p.m. per year. The decreases in silica probably are due, in part, to different analytical methods, although an increased supply of nutrients may have resulted in higher diatom populations and subsequent increases in silica.

Data presented by Powers *et al.*, (1959, Table 10) indicate appreciably greater increases in several of the ions. They compared the chemistry of the Detroit River for 1854, 1902, and 1897 (Lane, 1899), however, with determinations made at various water intakes in Lake Erie. Such a comparison is questionable, since the chemistry of the river is somewhat different from that of the lake (Tables 2 and 3). Furthermore, most of the change in concentrations of various ions noted in the lake is not found in the river water. Concentrations of sodium-plus-potassium and chlorides at the head of the Detroit River are the same today as in the past. Total solids, calcium, and sulfates have increased and silica has decreased (Table 3). Undoubtedly, considerable amounts of various ions are added to the waters of the river at and below Detroit. Sufficient information on the chemistry of a section of the river to make valid comparisons, however, is not available.

Dissolved oxygen

Very low dissolved-oxygen concentrations have been observed in recent years, but low

TABLE 3.—Concentrations (p.p.m.) of the major ions and total solids in the Detroit River

Item	1854 ¹	1882 ¹	1897 ¹	1934-38 ²	1946-48 ³	1948-49 ⁴	1957 ⁵
Calcium	20.0	24.8	24.8	27.5	—	28.0	30.7
Magnesium	—	7.4	6.1	8.0	—	8.0	—
Sodium and potassium	3.7	—	—	3.0	—	4.8	3.4
Silica	5.0	8.9	6.0	7.3	—	3.8	2.6
Sulfates	6.6	6.7	7.8	12.9	—	17.4	—
Chlorides	—	7.5	—	5.6	7.3	6.5	—
Total solids	98.1	117.1	114.4	118.6	141.0	131.0	—

¹ Lane (1899), City of Detroit water intake.

² Leverin (1947), average of five determinations between July 31, 1934, and March 23, 1938, Windsor, Ont., water intake.

³ International Joint Commission (1951), average of determinations made on transects from Windmill Point to Canadian shore at head of Detroit River (Table 21).

⁴ Thomas (1954), average of monthly determinations February 18, 1948, to January 14, 1949, Windsor, Ont., water intake.

⁵ Average concentrations in samples taken at 5-mile intervals from mouth to head of Detroit River, November 17, 1957, Bureau of Commercial Fisheries.

concentrations also occurred previously. The severity of oxygen depletion may, nevertheless, be somewhat greater at present than in the past. Because there is vertical turbulence in the shallow western basin, dissolved oxygen is usually around 80-percent saturation near the bottom, except during periods of thermal stratification such as occurred in 1953 (Britt, 1955a). Averages of the percentage saturation for bottom waters in 1928, 1929, and 1930 (Wright, 1955) are 83.5, 90.7, and 87.2. The average dissolved oxygen near the bottom in 1939 was 7.4 p.p.m., and at an average temperature of 19.8° C., the percentage saturation was 80.⁵ Our average percentage saturation was 80 in 1958.

If dissolved-oxygen concentrations alone are considered, conditions in the eastern basin appear to be much the same 30 years ago as they are today. The percentage saturation in the bottom waters averaged 60 to 70 in 1928 and 1929 (Fish, 1960), in 1950-51 (Powers *et al.*, 1959), and in 1957 (Bureau of Commercial Fisheries). Some very low dissolved-oxygen concentrations have been observed in the bottom waters of the central basin. The most recent and perhaps the severest oxygen deficit occurred in 1959 when oxygen could not be detected over extensive areas covering many square miles. We found an area with only 10-percent saturation in August 1958. Calculations of percentage saturations from data of Powers *et al.* (1959) for 1948, 1949, and 1950 give three low values of 35, 22, and

See footnote 2.

Average of results for sampling ranges P-1W and Table N-17 (International Joint Commission, 1959).

⁵ Calculations based on data presented by Chandler (1940) for May 9 through September; the 1928-30 observations covered a similar period.

35. Fish (1960) recorded two observations of 44- and 52-percent saturation in 1929. A low of 8.6-percent saturation was observed in 1930 at the western limits of the central basin (Wright, 1955). There is little information, however, on the extent both in time and area of these low concentrations. The recent occurrences of low oxygen concentrations may not, therefore, be indicative of a great change in the central basin. Average percentage saturation for comparable periods does, nevertheless, seem to be lower now than in 1929. The average percentage saturation in 1929 was 83.3; it was 67.4 during 1948-52 and 63.3 in 1958.⁶

Biochemical oxygen demand

The average biochemical oxygen demand (B.O.D.) has not changed appreciably since 1946-48 in the east end of the lake. It was 0.97 in the open lake in 1946-48 (International Joint Commission, 1951⁷) and 0.88 at the Buffalo, New York, water intake in 1957-58 (Public Health Service, 1958).

Nitrogen and phosphorus

Information is limited on the concentrations of nitrogen and phosphorus in Lake Erie. Such data as do exist are frequently questionable and difficult to interpret. Data compiled on nitrogen from the western basin seem, however, to be reliable and to show a trend. The average free ammonia in the island area increased from 0.013 p.p.m. in 1930 (Wright, 1955) to 0.036 p.p.m. in 1942 (Chandler and Weeks, 1945). An average of the International Joint Commission's records was 0.033 p.p.m. in 1946-48. Our 1958 average was 0.092 p.p.m. Nitrites increased from 0.005 p.p.m. in 1930 (Wright, 1955) to 0.008 p.p.m. in 1942 in the island area (Chandler and Weeks, 1945). Nitrates increased from 0.10 p.p.m. in 1930 (Wright, 1955) to 0.225 in 1942 (Chandler and Weeks, 1945). Our average total nitrogen for 1958 from stations around the islands was 0.83 p.p.m.; Chandler and Weeks (1945) recorded an average of 0.265 in 1942.

Data on nitrogen in the central and eastern basins show marked discrepancies. Determinations of free ammonia for 1901-03 (Lewis, 1906, 0.046 p.p.m.), 1925 (U. S. Corps of

Engineers, personal communication, C. p.p.m.), and for Erie, Pennsylvania, for 1958 (0.030 to 0.045 p.p.m.) indicate no change. Albuminoid ammonia decreased from 0.1 p.p.m. (Lewis, 1906) and 0.125 p.p.m. (U. S. Corps of Engineers) to 0.042 p.p.m. and 0.03 p.p.m. in 1956 and 1958. Nitrates increased from 0.085 p.p.m. in 1901-03 to 0.40 p.p.m. and 0.30 p.p.m. in 1956 and 1958. The average for free ammonia in 1928 (Fish, 1928) was 0.02 p.p.m., well below the figure of 0.045 p.p.m. at Erie, Pennsylvania, in 1958. Determinations for free and albuminoid ammonia, nitrites, and nitrates made at Cleveland water intake in 1910 and 1911 (Jackson (Wright, 1955) were essentially the same as those made in 1956-58 at Erie, Pennsylvania.

Phosphorus concentrations apparently increased. The magnitude of this increase is difficult to ascertain, since few determinations have been made for phosphorus and so doubt exists as to the exact unit in which they were recorded. The average total phosphorus in the island region in 1942 was 14.4 parts per billion (Chandler and Weeks, 1945). The average total phosphorus for this region found in the present study was 33 parts per billion in 1958 and 36 parts per billion in 1959. The average soluble phosphate-P content was 1.0 parts per billion during the last half of 1959 (Chandler and Weeks, 1945). An average of Curl's (1959) data for a comparable period in 1950 was 4.7 parts per billion.⁸

CONCLUSIONS

The bottom fauna and the fish fauna of Lake Erie have changed substantially. Increases have taken place in temperature, coliform bacteria, and in the concentrations of certain ions. Data on transparency, plankton, and dissolved oxygen, however, give no conclusive evidence of changes in Lake Erie. It is certainly doubtful whether the 1- to 2 p.p.m. increase in the concentrations of major ions is of any consequence to the biota. The seeming increases in the concentrations of nitrogen and phosphorus compounds, or, to the contrary, could be very important biologically and deserve further study. The type of change in the bottom fauna indicating an increase in the organic component of the sediments.

Any great changes in the chemistry of the plankton of the lake must originate in changes

⁶ Percentage saturation for 1948-52 calculated from University of Western Ontario data from station 2 (Powers *et al.*, 1959). The 1958 figure is based on data collected by the Bureau of Commercial Fisheries every 3 weeks at two stations northwest of Lorain, Ohio.

⁷ See footnote 4.

⁸ Based on data plotted in his Figure 4 for July and December, 1950.

the characteristics of the waters flowing in the lake, especially in the western basin are the great flow of the Detroit River is to an estimated flushing rate of about 2 mths. Information is needed on the chemical characteristics, past and present, of the Detroit River and other streams that flow into the Erie.

Our present knowledge of conditions in the lake suggests any trend toward eutrophication of Lake Erie can be detected best in the bottom in the western and central basins. The physical nature of the sediments influences the overlying water, but the effects may be important only during prolonged thermal stratification. Most of the changes in the bottom fauna seem to be confined to the western and central basins. A fauna similar to that of the upper Great Lakes exists in the region of Sandusky Point.

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Selective Breeding of Chinook Salmon

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ABSTRACT

Selective breeding of plants and animals has been carried on for hundreds of years. Few attempts, however, have been made to breed salmon that have characteristics which would better fit the fish for the needs of modern salmon management. Experiments started in 1949 at the University of Washington to develop a selected stock of chinook salmon (*Oncorhynchus tshawytscha*) have shown progress in producing fish better adapted to the environment available to them. Selected stocks grow faster, are more resistant to high temperatures and disease, mature earlier, and have a higher survival rate than the non-selected stocks.

INTRODUCTION

Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), historically were found in numbers in the large rivers entering the Pacific Ocean, from the Sacramento River north to the Yukon River. With the development of the West, the great rivers that were the ideal spawning and rearing areas for chinook salmon were used more and more by industry, often in conflict with the life processes of the fish.

The most productive chinook salmon river, the Columbia, has been the most widely used by industry of any of the major rivers which produce chinook salmon and has suffered the greatest decline in the fishery. The all-time production peak of over 42 million pounds was harvested in 1883 (Craig and Hacker, 1940). Since the peak year the yield of salmon has varied greatly from year to year but the over-all trend has been downward. The combined Oregon and Washington catch of chinook salmon for 1958 was 6,600,000 pounds (Washington Department of Fisheries, 1959).

Fisheries management agencies have been untiring in their efforts to halt the rate of decline. Restrictive regulations on fishing, pollution, and industrial development have been put into effect. Hatcheries have been built, blocked streams opened, fish ladders constructed at dams, and spawning channels built and put into use. To this impressive array of rehabilitation measures, we propose yet another area of effort—that of selective breeding.

PROBLEM OF INVESTIGATION

The major portion of the food used by man is now produced by plants and animals that have been selectively bred to produce greater

quantities of higher quality food. Salmon fish are especially suited to the technique of selective breeding, because the eggs can be spawned, fertilized with the sperm of selected males, and the best individuals can then be used for subsequent crosses. Strains of fish much better adapted to management exist than the wild fish have been developed using the techniques of applied genetics (Hayford and Embury, 1930; Lewis, 1930; Wright, 1951, 1952a, 1952b; Wolf, 1952; Donaldson and Olson, 1957; Donaldson, Hansler, and Buckridge, 1957).

In 1949 a program was initiated at the University of Washington using chinook salmon from the Soos Creek Hatchery, State of Washington Department of Fisheries, in an attempt to develop a strain that would be more productive than the stocks of fish available. After incubation the fish were reared to migratory size and marked by amputation of a fin. They were then released into Lake Union, from which point they migrated 4.6 miles through the lake and into Puget Sound. After feeding in the sea those that matured and survived returned to Puget Sound, to Lake Union, and finally up the small ladder to the ponds adjacent to the Fisheries Center on the University of Washington campus (Figure 1).

The objectives of the selective breeding program were to try to develop a strain of chinook salmon that would (1) return to ponds at the University; (2) mature and produce eggs after a short migration from the sea; (3) spawn at the desired season of the year; (4) mature at an early age; (5) produce maximum growth; (6) have a large egg yield; (7) have a high survival rate of eggs, fry, and fingerlings; (8) be resistant to disease; (9) migrate to sea at an early age; and (10) have a high survival rate in the



FIGURE 1.—Salmon rearing and collecting facilities at the University of Washington campus. The fingerlings are released into the small bay adjacent to the Union and the adults "home" up the ladder to the collecting area at the end of the long way.

Adult chinook salmon from the initial release in 1949 began to return to the collecting area at the College of Fisheries, University of Washington, (Figure 1) during the fall of 1955.

Subsequent transfers of eggs with the frequent release of the fingerlings into the Union produced returning adults to fill the remaining years. The return of 4-year-old adults to the ponds on the campus was only 0.1 percent of the fingerlings released. These adults produced twice the number of fingerlings required to maintain the run, allowing ample leeway for selection.

In the fall of 1955 a total of 48 fish returned from the 1952 brood year. These 3-year-old fish, 40 males and 8 females, were separated from the other age groups in the run. The eggs from the eight females were fertilized by the males of the same age group. After rearing, the fingerlings produced were marked by removal of the adipose fin and released to migrate to sea.

A total of 26,240 fingerlings from the 3-year-old parents were released into Lake Washington between May 1–7, 1956. At the time of planting the fingerlings weighed an average of 66 grams (97.4 to the pound) and were 10.2 centimeters in average standard length. During the fall months of October, November, and December, 1956, a surprising return of 12 precocious males of the spring release returned up the ladder to the ponds. The return of 1-year-old chinook salmon from the ponds must be a very rare occurrence, for in the records of the Hatchery Division of the State

of Washington Department of Fisheries not a single recorded incidence of such early maturity was found. The little yearling males accounted for 0.2 percent of the fingerlings released. The average fork length was 24.13 centimeters, and the range in length was 21.0 to 29.7 centimeters (Table 1).

In the fall of 1957 the precocious males of the 1955 brood year continued to return in numbers. A total of 227 returned up the ladder into the ponds. This return represented 0.87 percent of the fingerlings released. The fish had grown to an average length of 52.9 centimeters, the range being 38.0 to 63 centimeters.

A major portion of the returning population arrived during the fall months of 1958, with a total of 438 fish, 277 males and 161 females, or 1.67 percent of the 1955 brood-year fingerlings returning. The fish had grown to such a large size (Table 1, Figures 2 and 3) that it would have been impossible to tell them from the 4-year-old fish in the run except for the different marks made by removal of a specific fin on the fingerlings prior to release.

The normal 4-year cycle for this group of salmon was completed during the fall of 1959, when 135 additional fish returned, 30 males and 105 females. The total return of 852 fish from the sea to the ponds from a release of 26,240 fingerlings of the 1955 3-year-old parents was 3.25 percent, many times the expected return.

The lengths as measured from the tip of the snout to the fork of the tail for the chinook salmon returns of the 1955 brood year are grouped by years and plotted in Figure 2. The progression of the modes each year is indicative of the rate of growth of the fish. For the three returns the growth progressed at a fairly uniform rate, 24.2 centimeters in 1956, 52.9 centimeters in 1957, and 75.73 centimeters in 1958. The fish returning in 1959, however, averaged only 79.95 centimeters. This marked change in the rate of length increase may indicate a separation of the fish in the sea, with the more rapidly growing fish returning early and the slower-growing portion of the population maturing and returning in the fourth year.

The development of a brood stock which will produce large numbers of high quality eggs should be a major objective in any program of selective breeding. Rounsefell (1957) records the average chinook salmon egg production at 5,449 for fish from the Sacramento

TABLE 1.—Summary of the returns of the 1955 brood-year chinook salmon to the ponds at the University of Washington¹

Return year	Number of fish returning	Percentage return of released fingerlings	Sex	Fork length (centimeters)		Weight (pounds)	
				Mean	Range	Mean	Range
1956	52	0.2	Male	24.1	21.0–29.7	—	—
1957	227	0.87	Male	52.9	38.0–63.0	—	—
1958	277	1.67	Male	76.0	51.0–89.0	—	—
	161		Female	75.3	65.0–86.0	—	—
1959	438	0.51					
	30		Male	80.0	63.0–92.0	12.8	6.9–26.9
	105		Female	79.9	61.0–94.0	15.4	6.3–24.1
	135						
Total	852	3.25	—	—	—	—	—

¹ 1955 brood-year fingerlings from 3-year-old parents were marked by removal of the adipose fin and released in Lake Union, May 1–7, 1956. The 26,240 fingerlings had an average weight of 4.66 grams and a standard length of 6.67 centimeters.

River, California; 3,753 for the Klamath River, California; and 3,885 for the Cowichan River, British Columbia.

The number of eggs produced by the 3-year-old females at the University of Washington was determined for 108 of the 161 fish available. The average number of eggs was 3,975, with a range of 2,451 to 5,460

(Table 2). The eggs of these fish averaged 8.06 millimeters in diameter and 66.24 to 100.00 liquid ounce.

The number of eggs produced by 89 of 105 females that returned in 1959 was determined. The average number was 4,171, with a range of 2,010 to 5,700. The difference between the mean average number of eggs produced by the 3-year-old female fish

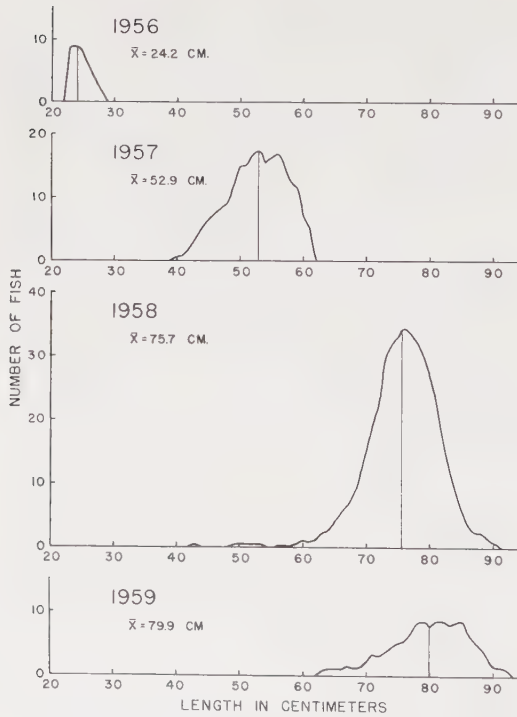


FIGURE 2.—Length distribution of the 1955 brood-year chinook salmon that returned to the collecting ponds at the University of Washington. (Fork length smoothed by a moving average of five).

TABLE 2.—Egg production by 3- and 4-year-old female chinook salmon from the 1955 brood-year returning to the ponds at the University of Washington

Fork length (centimeters)	3-year females		4-year females	
	Average number of eggs	Number of fish	Average number of eggs	Number of fish
62	—	—	2,010	—
63	—	—	—	—
64	2,847	1	2,546	—
65	2,451	1	—	—
66	—	—	2,808	—
67	—	—	2,679	—
68	—	—	—	—
69	3,465	2	—	—
70	3,780	4	—	—
71	4,043	4	3,990	—
72	3,585	4	4,056	—
73	3,985	5	3,545	—
74	3,707	15	4,016	—
75	4,126	15	3,489	—
76	3,804	13	3,705	—
77	4,170	14	3,530	—
78	3,828	11	4,281	—
79	4,079	5	4,153	—
80	4,550	3	4,078	—
81	4,580	3	3,922	—
82	4,328	3	4,500	—
83	4,470	2	4,518	—
84	—	—	4,399	—
85	5,460	1	4,702	—
86	4,560	1	4,747	—
87	—	—	5,007	—
88	—	—	—	—
89	—	—	4,970	—
90	4,368	1	—	—
91	—	—	5,700	—
92	—	—	—	—
93	—	—	5,415	—
94	—	—	4,959	—
Mean average or total	3,975	108	4,171	—



FIGURE 3.—Three-year-old male chinook salmon turning up the ladder into the collecting area of ponds at the University of Washington.

4-year-old fish was significant ($t_{.95} = 0.75$ with 195 degrees of freedom). The males from the 4-year-old females were also slightly larger than those from the 3-year-old; the average was 8.30 millimeters in diameter and 61.33 eggs to the liquid ounce. In general the number of eggs produced by the females of both age groups increased with the length of the fish (Table 2, Figure 4). The average increase in number of eggs for each centimeter increase in fork length of male over the range of the spawning adults (60–94 centimeters) was 89 eggs. The variation in numbers of eggs within each length-group was so great, however, that before making the selection of the most productive males for continued brood-stock development, it is essential that the number of eggs from each female be determined.

SUMMARY AND CONCLUSIONS

An annual run of chinook salmon has been developed that returns to the ponds on the University of Washington campus in sufficient numbers for selective breeding experiments. In the regular run, most of the fish returning are 4 years of age and have a total survival of about 0.1 percent of the finger-

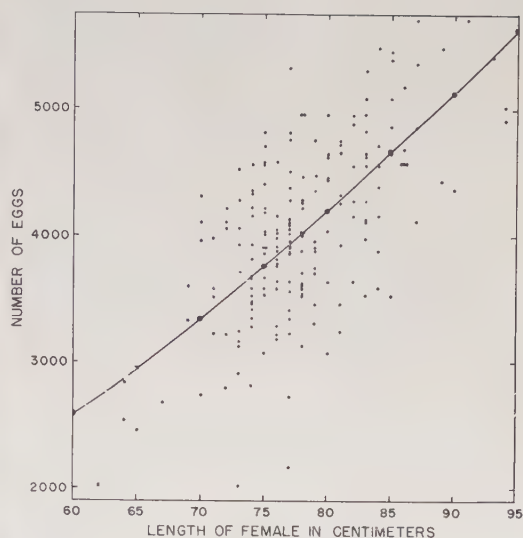


FIGURE 4.—Length-fecundity relationship of chinook salmon females of the 1955 brood year that returned to the ponds at the University of Washington during the fall months of 1958 and 1959. (Log $Y = 0.3756 + 1.706 \log X$, where X is the length of the female in centimeters and Y is the number of eggs produced.)

lings released. A few 3-year-old fish, which returned during the fall of 1955, were isolated from the rest of the population, spawned, the eggs incubated, and the fingerlings reared and marked by amputation of the adipose fin, before being released into Lake Union for migration to Puget Sound and the north Pacific Ocean. The return of adult fish from the sea to the ponds on the campus far exceeded the normal expectancy. The total was some 30 times that of non-selected stocks. The number of eggs produced by the returns in the third year alone was sufficient to increase the planting of very select fingerlings tenfold—26,240 in 1956 to 261,154 in 1959—and to provide a large excess of fingerlings for the regular stocking program. By taking advantage of the natural variation that occurs in stocks of fish and selecting those with characteristics most useful in our management attempts, it has been possible to increase the yield manyfold.

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Measurement of Potential Fishing Quality

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ABSTRACT

The commonly used "average catch per hour" does not provide a satisfactory measure of the quality of sport fisheries because of the extreme variation in the efficiency of the angler hour. A catch rate calculated from that portion of the data which comprises the more efficient effort units is a more precise statistic, and is probably more closely related to the actual condition of the fishery and to the effects of management. Three examples of creel census data are used to illustrate a suggested method for calculating this measure of potential fishing quality, and a standardized notation for presenting the results is recommended.

Measures of the quality of sport fisheries are important in evaluating the effects of management. They should be definite attributes of the water areas so that changes in fishing quality will be reflected faithfully by the measures used. This requirement implies that some feature of the particular water must be compared to a definable, unchanging standard. The average hour of angling effort has been widely accepted as this standard, and the measure is the average catch per hour of fishing computed from the catches of all fishermen interviewed. This measure is unsatisfactory to describe the fishing quality that a fishery is actually capable of providing. The present paper describes a new method for calculating catch-per-unit-of-effort which eliminates all but the most successful fishing trips and, therefore, describes the potential fishing quality.

Catch-per-unit-of-effort as a measure was originated to describe conditions in marine commercial fisheries where a unit of effort by a professional fisherman using commercial gear could be considered relatively standard. The hour of angling exerted on a lake or stream by an amateur fisherman, however, cannot be considered an analogous unit. Many creel censuses have demonstrated the great variation in the nature of the angler effort. As few as 25 percent of the anglers may catch as many as 80 percent of the fish (Edham, 1949). The percentage of completely unsuccessful angling trips often exceeds 50 (Rupp, 1955), and at particular unfavorable times, even the expert fishermen catch nothing.

The reasons for poor catches are many and variable. Catches may be poor because the availability of fish in the stream or lake is low, or because factors which are unrelated to the condition of the fish population are

operating. These factors may be inexperience, inattention, interference, unfavorable time of day, unfavorable weather, or many other factors.

If the relative importance of the various factors contributing to poor catches remained constant in various waters and at different times, it might be reasonable to assume that the average catch per angler hour could still be used as a standard. This condition is probably seldom met. Novices make up variable proportions of the total anglers depending upon time of year, weather, stocking, newspaper accounts of good catches, and other factors. Many inexperienced anglers lose interest as the season progresses. Novices may predominate on waters near cities and towns, but be less numerous on remote waters. It is therefore possible to get different catch-per-unit-of-effort values from two waters of equal fishing quality if one is remote and the other is near a center of population.

Considerable improvement in comparison of fishing quality on different bodies of water or at different times can be accomplished if the potential fishing quality is measured, rather than the average return to the angler. Potential fishing quality may be defined as the catch-per-unit-of-effort which the water provides for experienced anglers who fish when conditions are favorable. If estimates are made only from the data on catches which fulfill these requirements, much of the variability in catch rate which results from inefficient angling can be eliminated, and the resulting measure will be a truer index to the actual status of the fishery.

A satisfactory method of eliminating inefficient units of fishing effort is a major problem. Any attempt to classify the relative skill of anglers would be highly subjective, and it is difficult to predict or define favorable fish-

TABLE 1.—Distribution of trout caught per trip and total recorded catch during partial creel census at Sunkhaze Stream, Maine, during 1951 and 1952

Catch per trip	Number of trips	Number of trout
1951		
0	344	0
1	57	57
2	25	50
3	15	45
4	18	72
5	13	65
6	2	12
7	5	35
8	1	8
9	2	18
10	3	30
11	1	11
12	0	0
13	0	0
14	0	0
15	1	15
16	0	0
17	1	17
Total	488	435
1952		
0	384	0
1	59	59
2	40	80
3	23	69
4	20	80
5	9	45
6	7	42
7	7	49
8	4	32
9	2	18
10	4	40
11	6	66
12	2	24
13	0	0
14	3	42
15	7	105
Total	577	751

ing conditions. An objective way to identify the efficient units of effort would be on the basis of their results. The fishing trips which resulted in the best catches probably occurred when experienced anglers fished at favorable times. The poorer catches from any particular water are basically the result of angling inefficiency, either a deficiency in skill or a poor choice of the time and place for angling.

Non-standard fishing units are not eliminated entirely by selecting the better catches. Poor anglers who fish at favorable times may make good catches, and skilled anglers who fish when conditions are poor may make good catches. Nevertheless, the variability will be greatly reduced by selecting the better catches, and the resulting catch-per-hour will be a better measure of the actual fishing quality than when all catches are included.

A method of selecting the units of fishing effort which resulted in the better catches was

developed by use of data from weekend holiday creel censuses at Sunkhaze Stream, Maine, during 1951 and 1952 (Rupp, 1951). Frequency distributions of the catch of eastern brook trout, *Salvelinus fontinalis*, show that there was more fishing effort, a larger total catch, and considerably more large individual catches in 1952 (Table 1). The increase in number of large catches suggests that fishing quality may have been better in 1952, but this assumption would have to be tested by calculating catch-per-unit-of-effort and attendant measures of variability.

The following three methods of calculating catch-per-unit-of-effort were chosen: (1) catch per hour for all fishing trips; (2) catch per hour computed for successful fishing trips only; and (3) catch per hour computed from trips which provided approximately the total catch in the largest individual bag. Approximately half of the total recorded catch was provided by 5.94 percent of the fisherman trips in 1951, and by 6.07 percent of fisherman trips in 1952. A fishing trip defined as fishing effort expended by a fisherman on one calendar day. The weighted average catch-per-hour, variance, standard error, limits of the 90 percent confidence interval, and the precision of the estimate at 90 percent confidence were computed for each of the 2 years and for each of the three analytical methods (Table 2). The first method is the traditional one involving the average catch per hour for all units of effort. The second and third methods provide two measures of potential fishing quality, each restricted in a different way.

There is a marked difference between the potential fishing quality of the stream in 1951 and 1952. The potential fishing quality measured by Method 3, and the average fishing quality measured by Method 2, were approximately five times as high as the fishing quality experienced by the average fisherman in 1951 as compared with 1952. The potential fishing quality was almost 1.5 times as high in 1952 as in 1951.

The difference in fishing quality between the two years as indicated by each of the three methods was tested with *t*, using 90 percent confidence limits as a criterion of reliability. The differences between estimates of potential fishing quality by Method 3 are statistically significant at the 98 percent level, the differences between the estimates by Method 2 are significant at the 90 percent level, and the differences between estimates of average fishing quality are not significant. The precision

TABLE 2.—A measure of average fishing quality and two measures of potential fishing quality for eastern brook trout at Sunkhaze Stream, Maine, during 1951 and 1952

Method	1951			1952			t
	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision ¹ of estimate (percent)	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision of estimate (percent)	
	0.359	0.282–0.436	± 21.4	0.424	0.318–0.530	± 25.0	0.86 (<i>p</i> = 0.40, 76 d.f.)
	0.796	0.691–0.901	± 13.2	1.002	0.847–1.157	± 15.5	1.86 (<i>p</i> = 0.10, 65 d.f.)
	1.549	1.279–1.819	± 17.4	2.239	1.864–2.614	± 16.7	2.62 (<i>p</i> = 0.02, 30 d.f.)

¹The precision of an estimate may also be known as the error of an estimate expressed as a percentage. For Method 1, 1951, the limits of the 90 percent confidence interval are 21.4 percent above and below the point estimate or weighted average.

estimates of potential fishing quality is considerably greater than the precision of the estimates of average fishing quality. Selection of the more experienced anglers who fished when conditions were more favorable reduced the variability of the data and allowed a more precise evaluation of the fishing quality which the stream is capable of providing.

The precision of the estimates obtained by Method 2 is slightly greater than that obtained by Method 3, but this improvement is probably no more than a reflection of the greater number of degrees of freedom associated with Method 2. Method 3 is recommended for use wherever possible because it is much more effective for efficient angling units and provides a higher and more sensitive measure of potential fishing quality.

The quality of sport that an angler experiences involves more than the number of fish caught and the rate of catch. A large number of fish caught at a high rate per hour might be considered poor fishing if the fish were small. A small catch obtained at a low rate might be highly satisfactory if the fish were large. To provide a description of fishing quality that can be compared more logically from water to water and from time to time, it is essential that both catch rate and average size of the fish be included. The following plan for standardized presentation of these measures for potential fishing quality, using Sunkhaze Stream data as an example, is recommended.

1951—1.549 ± 17.4%; 8.00" total length

1952—2.239 ± 16.7%; 7.96" total length

The catch rate is the weighted average catch per hour computed by Method 3, accompanied plus/minus its precision as described by the limits of the 90 percent confidence interval expressed in percent.

The field data from the Sunkhaze Stream censuses were recorded in such a way that the catch and effort of each individual fisherman on each day could be determined. It is often more convenient, however, to record catch and effort by party rather than by individual. With data in this form, the selection of the more successful trips is more difficult because they cannot be grouped into a single frequency distribution. A party of two anglers who catch six fish cannot be assigned the same position in a frequency distribution as a party of six anglers who catch six fish. This difficulty can be overcome by selecting from a family of frequency distributions. An illustration is provided by data from Foye¹ which were taken during a census of the fishing for smallmouth bass, *Micropterus dolomieu*, at Long Pond, Maine, during 1952. Size-frequency distributions of catches were constructed for parties of one, two, three, etc. These distributions were then collected and entered in a table (Table 3) by means of a scaling system which places all catches which are of equal value on the same line of the table. For example, a catch of one fish by a party of one man is equivalent to a catch of two fish by a party of two men, and, therefore, the total catches in these categories can be added. The horizontal summation of all analogous catches is then entered in the last column, and the last column is added to give the total recorded catch and to serve as the basis for selection of the effort units which resulted in approximately half of the total. Half of the total recorded catch at Long Pond was made by parties of one who caught more than two fish, parties of two who caught more

¹ Foye, Robert E. (1954) A study of the freshwater fisheries of Long Pond and Great Pond of the Belgrade Chain of Lakes in central Maine. Rept. Maine Dept. Inland Fish. and Game, Augusta, Maine. 20 pp. (Mimeo.)

TABLE 3.—*Catch per trip (TC), number of trips (T), and catch of bass (B) recorded by party size for Long Pond, Maine, 1952*

Size of party															Total catches			
1			2			3			4			5				Other parties		
TC	T	B	TC	T	B	TC	T	B	TC	T	B	TC	T	B		TC	T	B
—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	1
—	—	—	—	—	—	—	—	—	1	11	11	—	—	—	—	—	—	11
—	—	—	—	—	—	1	33	33	—	—	—	—	—	—	3	1 ¹	3	36
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
—	—	—	1	101	101	—	—	—	2	5	10	2	1	2	—	—	—	111
—	—	—	—	—	—	2	24	48	—	—	—	—	—	—	—	—	—	48
—	—	—	—	—	—	—	—	—	3	3	9	—	—	—	—	—	—	9
1	30	30	2	53	106	3	9	27	4	2	8	—	—	—	14	1 ²	14	185
—	—	—	—	—	—	4	10	40	—	—	—	—	—	—	—	—	—	40
—	—	—	3	25	75	—	—	—	—	—	—	—	—	—	—	—	—	75
—	—	—	—	—	—	5	5	25	—	—	—	—	—	—	—	—	—	25
—	—	—	—	—	—	—	—	—	7	1	7	—	—	—	—	—	—	7
2	13	26	4	16	64	6	3	18	—	—	—	—	—	—	—	—	—	108
—	—	—	—	—	—	7	2	14	—	—	—	—	—	—	—	—	—	14
—	—	—	5	4	20	—	—	—	10	1	10	—	—	—	—	—	—	30
—	—	—	—	—	—	8	2	16	—	—	—	—	—	—	—	—	—	16
3	4	12	6	6	36	9	1	9	12	1	12	—	—	—	—	—	—	69
—	—	—	—	—	—	—	—	—	13	1	13	—	—	—	—	—	—	13
—	—	—	7	3	21	—	—	—	—	—	—	—	—	—	—	—	—	21
4	2	8	8	5	40	12	1	12	—	—	—	—	—	—	—	—	—	60
Other catches															316			1,197
Total																		

¹ Party of 9
² Party of 14
³ 64 fish from two-angler parties catching four fish per trip were included with total of parties catching more than two fish per person per trip to permit division into approximately 50 percent groups.

than three fish, parties of three who caught more than six fish, and parties of four who caught more than seven fish. These are the data to be selected from the original field notes for calculation of weighted average catch per hour, the measure of potential fishing quality designated as Method 3.

In addition to describing the method by which party data may be sorted for analysis, the Long Pond data also illustrate a difficulty which will probably be encountered often when creel census records are made on a party basis. In order to approximate a 50 percent division of the total recorded catch, it was necessary to include the data provided by parties of two who caught four fish, while, at the same time, rejecting data from parties of one who caught two fish and parties of three who caught six fish. An arbitrary division of the analogous catch of 108 fish was required.

If the individual members of different-size parties can be assumed to have approximately equal success rates, arbitrary selection of parties of an analogous catch should have no effect on the utility of the above method. This assumption, however, is probably not justified in most cases. The observation that most of the fish are quite often taken by a small number of fishermen can logically be extended to situations where anglers fish together in parties, since a party's catch is seldom the result of equal contribution by all its members. The failure of this assumption has the effect of increasing the variable quality of the hour of angling effort, and must, therefore, be responsible for a decrease in the value and accuracy of the catch-per-unit-of-effort as a measure of fishing quality. More reliable results can be obtained if the catch and effort of each fisherman are recorded.

TABLE 4.—*Average fishing quality and potential fishing quality for smallmouth bass at Long Pond, Maine, in 1952 and at Great Pond, Maine, in 1953*

Method	Long Pond			Great Pond			<i>t</i>
	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision of estimate (percent)	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision of estimate (percent)	
1	0.161	0.127–0.195	± 21.1	0.150	0.120–0.180	± 20.2	0.58 (<i>p</i> > 0.5, 73 d.f.)
3	0.854	0.687–1.021	± 19.6	0.677	0.594–0.760	± 12.2	1.67 (<i>p</i> = 0.2, 34 d.f.)

TABLE 5.—Measures of average and potential fishing quality for landlocked salmon at Square Lake, Maine, 1958 and 1959

Method	1958			1959			t
	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision of estimate (percent)	Weighted average catch per hour	Limits of 90 percent confidence interval	Precision of estimate (percent)	
	0.090	0.061–0.119	± 32.2	0.077	0.042–0.112	± 45.4	0.52 ($p > 0.5$, 20 d.f.)
	0.339	0.300–0.387	± 11.5	0.331	0.278–0.384	± 16.0	0.22 ($p > 0.5$, 19 d.f.)

Despite the inherent disadvantages of partial creel census, potential fishing quality may still be estimated (Table 4). Values of average and potential fishing quality for smallmouth bass in Great Pond, Maine, in 1953² are also added for comparison. Potential fishing quality as calculated by Method 3 was roughly 4 times as high as the fishing quality experienced by the average fisherman. There were also notable increases in the precision of estimates obtained by Method 3. In these cases, however, the increases in precision were not great enough to make the difference between potential fishing quality at Long Pond in 1952 and at Great Pond in 1953 significant at the 90 percent level.

Putting these measures in standard form, potential fishing quality for smallmouth bass in the two waters during the 2 years was:

Long Pond, 1952— $0.854 \pm 19.6\%$;
13.6" total length;

Great Pond, 1953— $0.677 \pm 12.2\%$;
14.3" total length.

The foregoing examples have come from waters where fisheries in which catches are often as high as 15 or more fish per man per day. In other situations, however, catches cannot be so high because there are legal restrictions or other reasons. The question, whether a partial creel census is a valid method of analysis which involves discarding part of the catches and most of the effort, can be used in these cases, therefore, is not clear. This question has been investigated by using data from a partial creel census of fishing for landlocked salmon, *Salmo salar*, at Square Lake, Maine, in 1958 and 1959.³ The recorded salmon catches during these years were relatively low (477 fish in 1958; 220 in 1959), and the highest catch per man per day did not exceed five fish.

The Square Lake creel census data were analyzed by Methods 1 and 3 (Table 5). Calculation by Method 3 resulted in catches per hour approximately four times as high and approximately three times as precise as those obtained by Method 1.

In standard form, the results of the censuses were:

1958— $0.339 \pm 11.5\%$; 17.4" total length;

1959— $0.331 \pm 16.0\%$; 17.4" total length.

In the analysis of the 1959 census, data from 573 anglers who caught 220 fish were used for calculation by Method 1, and data from 63 anglers who caught 103 fish were used for calculation by Method 3. Thus precision was increased approximately three times by using Method 3 rather than Method 1, while, at the same time, use of Method 3 required discarding almost 90 percent of the effort units and slightly more than 50 percent of the total recorded catch. This result is particularly striking in view of the small numbers of effort units and fish originally available.

Restricting the analysis of creel census data to the catches and efforts of the more successful anglers results in an important reduction of variability in the efficiency of the angling hour, and a concomitant increase in the accuracy and usability of the results.

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¹ See footnote 1.
² Original field data were loaned from the files of Kendall Warner, Regional Fishery Biologist, Maine Department of Inland Fisheries and Game, Ashland, Maine.

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Records, Ages, and Growth of the Mooneye, *Hiodon tergisus*, of the Great Lakes

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ABSTRACT

Mooneyes (*Hiodon tergisus*) are very scarce in the upper three Great Lakes since only four specimens have been received from Lake Michigan, one from Lake Huron, and none from Lake Superior. The published statistics of the mooneyes are erroneous. Those of 1931 of Lake Michigan were perhaps chubs (*Coregonus* spp.) and those of Lake Huron of 1929 were also chubs and of 1934, 1949, and 1951 were gizzard shad (*Dorosoma cepedianum*) but since 1956 were alewives (*Alosa pseudoharengus*). Mooneyes are common in Lakes Erie and Ontario and perhaps in Lake St. Clair but are commercialized only in the States of Ohio and Michigan. Virtually all Lake Erie mooneyes were caught in trap nets, pound nets, and seines in less than 35 feet of water. Their life-history data collected in 1927-31 included lengths and weights of age-groups I-VII, calculated increments and lengths based on both anterior radii and lateral diameters of scales, length-weight relationships, and sexual maturity. Apparently mature specimens exceeded 8.8 inches, 3.25 ounces, and age-group I.

On September 12, 1943, a female mooneye (*Hiodon tergisus*) was received from Cyril A. Nelson, a Michigan conservation officer. Al Thompson, a commercial fisherman of Rogers City, Michigan, had caught the specimen in a 6-foot shallow trap net which had been set in 12 feet of water one-half mile from the range lights of Presque Isle Harbor, Lake Huron. The mature mooneye measured 14 inches total length, weighed 14.2 ounces, hatched in 1935, and belonged to age-group VIII. It has been deposited in the Museum of Zoology, University of Michigan (Cat. No. 177274). So far as is known, this mooneye is the first one and the only one taken from Lake Huron.

Radforth (1944) recorded on a map mooneyes in western Lake Superior, Georgian Bay, and off the northern point of Bruce Peninsula in Lake Huron proper (an error was made in the legend of the figure: actually No. 2 locates mooneyes, No. 3 goldeyes). The author reported that the details of the total distributions of these two species had been dealt with by Kerswill¹ and several new records had extended the range of the goldeye (*Hiodon alosoides*).

At my request Dr. J. R. Dymond examined Kerswill's manuscript and found no occurrence of the mooneye in Lakes Huron and Superior. He also consulted John Budd, who stated that no one of his staff had ever taken

or seen a mooneye in South Bay, Manitowish Island, or in Georgian Bay. Neither the literature listed by Radforth nor Van Oosten (1957) extensive bibliography of the Great Lakes publications revealed any record of a mooneye in Lakes Huron and Superior. Radforth had seen the records or specimens of mooneyes from these lakes she should have referred to the sources of information.

The published statistics of the mooneyes in the Great Lakes or of the gizzard shad (*Dorosoma cepedianum*) and alewives (*Alosa pseudoharengus*) are not always reliable. It is well known that many commercial and sport fishermen used the name "mooneye" not only for the real mooneyes but also for the gizzard shad and alewives because these three species are similar in general appearance, having a silver-colored and slab-sided body with a narrow belly.

Years ago, and probably even now, certain chubs (ciscoes) were also called "mooneyes" because they had comparatively large eyes, especially the kiyis (*Coregonus kiyi*). The 1931 United States record of 6,105 pounds of mooneyes caught in gill nets from the Wisconsin waters of Lake Michigan, although mooneyes had never been listed in the statistics of Lake Michigan in any other year, may be in error. Later it will be shown that mooneyes have seldom been caught in gill nets at depths below 35 feet where most of the Lake Michigan gill nets have been operated.

Genuine mooneyes inhabit Lake Michigan but apparently are rather scarce. The valid records actually revealed wide distribution

¹Kerswill, J. C. (1937) A taxonomic and distributional study of *Amphiodon alosoides* and *Hiodon tergisus*. M.A. Thesis, University of Western Ontario.

of the species. The first specimen, an adult 214 millimeters standard length, was submitted for identification on June 1, 1922, to Smith Brothers, Port Washington, Wisconsin. The details of the other specimens are as follows: September 17, 1938, from a pound net at Gladstone, Michigan, sent by Roy Jensen; July 6, 1941, from a pound net at Saukville, Michigan, an adult 253 millimeters standard length, sent by Frank Sewers; January 31, 1944, from a fyke net in 35 feet of water south of Saunders Point, Gladstone, Michigan, mature male, 259 millimeters standard length, 318 millimeters (12.5 inches) total length, sent by Roy Jensen.

The first Lake Huron statistics of so-called mooneyes were published by the United States showing that 2,895 pounds, valued at \$21.00, were taken in 1929, but the State of Michigan listed these fishes as shiners. Michigan also reported shiners from Lake Erie in 1929 that were again named mooneyes by the United States. These fishes totaled 701 pounds, valued at \$21.00. The price per pound of these Lake Erie fishes averaged 3 cents but those from Lake Huron averaged 10 cents. It was determined that the only other species from Lake Huron that brought 10 cents per pound was the chub (*cisco*) and in Lake Huron only the mooneyes brought 3 cents per pound. These 1929 prices indicate that the aforementioned Lake Huron specimens were really "mooneye" chubs and the Lake Erie fishes were real mooneyes.

The next Lake Huron record of mooneyes was published by the United States listed 330 pounds caught in 1934 north of Lexington, Michigan. These fishes, however, were identified as gizzard shad. The State of Michigan did not include these fishes either as mooneye or gizzard shad in its published statistics. Until 1949 were mooneyes again reported from Lake Huron when 52 pounds were reported from the Saginaw Bay area. Perhaps the average prices may again identify these mooneyes as gizzard shad. Mooneyes were sold for 5 cents per pound, shad for 2 or 3 cents. Since the prices of both the mooneyes and gizzard shad of Lake Huron averaged 2 cents per pound, all of these fishes were not real shad. In 1951 mooneyes that weighed only 1 pound were again recorded from Saginaw Bay although not identified by authority.

The next statistics of Lake Huron mooneyes indicated an increasing yield from 255

pounds (actually 875 pounds) in 1956 to 13,663 pounds in 1958 when it surpassed the maximum reported production of gizzard shad (6,483 pounds). All of these mooneyes were taken from Saginaw Bay by certain fishermen of one of the companies, although the rest of the companies as well as other fishermen listed only gizzard shad. Gizzard shad were caught on the same grounds where the mooneyes were taken. It is of interest to note that the United States research vessel *Cisco* had not taken a single mooneye in 1956 in the experimental nets operated in Saginaw Bay and southern Lake Huron. However, tremendous numbers of alewives were caught. I have now been informed (spring, 1960) that the alewives of Saginaw Bay had actually been called mooneyes since 1956.

The facts that the gizzard shad had been taken from Lake Huron off Sarnia, Ontario, as early as 1877 (Wilmot, 1879) and commercialized every year since 1938 indicate that the reported mooneyes were usually gizzard shad, although recently were alewives. The statistics did not reveal the abundance of these Lake Huron shad and alewives because most of them had not been marketed. Swarms of gizzard shad had already been observed before the years when they had been sold, as for example, in Georgian Bay 1919, in Saginaw Bay 1920, 1932, 1933, and 1937, off Alpena, Michigan, 1932 and 1933, in Lake St. Clair and St. Clair River 1932 and 1933, off Goderich, Ontario, 1933, and off Harbor Beach, Michigan, 1933. When they suddenly increased in numbers, they periodically underwent heavy mortality.

The real mooneyes of the Great Lakes are most abundant in the Ohio waters of Lake Erie. They were listed in published statistics for the first time in 1899 at 43,836 pounds, the maximum record. Thereafter statistics were published for the years 1918-21, 1927 (Michigan), and continuously from 1929. The Lake Erie annual catch averaged 5,441 pounds during 1918-21, 12,753 pounds during 1929-56, and only 500 pounds in each year of 1957 and 1958, the minimum production. Whether the early statistics of the mooneyes had included gizzard shad may be somewhat doubtful because the production of the shad had not been recorded until 1935, although not every year thereafter.

Scientific records indicate that mooneyes are also rather common in Lake Ontario and the St. Lawrence River, but they apparently have not been marketed since they have not

TABLE 1.—*Ports, dates of capture, and number of Lake Erie mooneyes in various age groups, 1927–29*

[Number of specimens in parenthesis may have been taken from more than one location]

Age group	Number of fish	Ports	Periods of capture
I	31	Sandusky, O.	Sept. 15—Nov. 5, 1927 (19)
		Huron, O.	Aug. 10—Nov. 27, 1928 (9)
		Conneaut, O.	May 15, 27, 1929 (3)
II	5	Sandusky, O.	Sept. 15—Oct. 31, 1927
III	9	Sandusky, O.	Aug. 26—Sept. 26, 1927
IV	5	Toledo, O.	Sept. 12, 1927 (1)
		Sandusky, O.	Nov. 13, 27, 1928 (4)
V	7	Toledo, O.	Aug. 19—Sept. 15, 1927 (4)
		Sandusky, O.	Nov. 13, 27, 1928 (2)
		Vermilion, O.	May 15, 1929 (1)
VII	1	Toledo, O.	Nov. 13, 1928
2.24 ¹	58 ²	All ports	1927–1929

¹ The average number of annuli of all age groups.
² Two of age-group III, one of IV, and one of V were taken in 1927 in shoal gill nets; one of V caught in 1927 in a bullnet; all other specimens were taken in trap nets.

been listed in the United States statistics unless included in the miscellaneous species that were published in the 18 years during the period from 1879 to 1928.

Very little information has been published about the life history of the Great Lakes mooneye, the only species of its family in

these lakes. Boesel (1938) listed the stomach contents of Lake Erie mooneyes. The smaller than 40 millimeters had contained Entomostraca and the larger individuals (133 millimeters) had consumed insects and amphipods. Johnson (1951) reported general information on 650 mooneyes from Lake Erie and Lake St. Clair. His data showed a length from 7 to 13½ inches, weights from 18 ounces, ages from 1+ to 8+ years, eggs from 10,000 to 20,000 per female. Stomachs contained aquatic and terrestrial invertebrates, mostly insects. Spawning occurred in April and May. Trautman (1957) recorded that the young-of-year mooneyes of Lake Erie ranged from 4.5 to 6.5 inches in October. Adults usually varied from 11.0 to 15.0 inches and from 12 ounces to 2 pounds. He did not indicate that all of these measurements were applied to the Lake Erie mooneyes. During the Lake Erie investigations mooneyes were recorded in the samples of 1927–31, and detailed data and scales were collected.

Our records indicate that the mooneyes were not abundant in Lake Erie and virtually all were caught in trap nets, pound nets, or seines in depths less than 35 feet. Only one specimen was taken in a bullnet in 42 feet of water and four in shoal gill nets in depths

TABLE 2.—*Standard and total lengths, weights, and calculated standard lengths based on radius and diameter measurements of the age groups of Lake Erie mooneyes, 1927–29*

[Specimens of different years and ports have been combined; numbers of specimens in parentheses]

Age group	Number of fish ¹	Average standard length (millimeters)	Computed total length (inches) ²	Average weight (ounces)	Average calculated standard lengths for each year computed from scale dimensions					
					1	2	3	4	5	6
I	31	177	8.4	2.91	Radii ³ Diameters ³	91 106				
II	5	203	9.6	4.25	Radii Diameters	97 114	159 166			
III	9	244	11.6	8.06	Radii Diameters	87 106	173 181	220 222		
IV	5	257	12.2	10.30	Radii Diameters	81 95	156 168	203 207	236 239	
V	7	265	12.6	11.18	Radii Diameters	73 90	151 160	199 203	234 236	254 255
VII	1	276	13.1	12.75	Radii Diameters	77 82	170 181	219 215	237 242	254 252
2.24 ⁴	58 ⁵	209	9.9	5.63	Radii Diameters	87 103	161 170	210 212	235 238	254 255
						(58)	(27)	(22)	(13)	(8)
Total length (inches)					Radii Diameters	4.1 4.9	7.6 8.1	10.0 10.1	11.1 11.3	12.0 12.1
Increments (inches)					Radii Diameters	4.1 4.9	3.5 3.2	2.3 2.0	1.2 1.2	0.9 0.8
Increments (millimeters)					Radii Diameters	87 103	74 67	49 42	25 26	19 17

¹ Sexes were combined since only six males and nine females were recorded.
² Standard length $\times$ 1.206 equals total length.
³ Radius of anterior section and diameter of lateral areas.
⁴ The average number of annuli of all age groups.
⁵ See footnote 2, Table 1.

TABLE 3.—Length-weight relationship of the Lake Erie mooneyes, 1927–31

Average total length (inches)	Average total length (inches)	Average standard length (millimeters)	Average weight (ounces)	Number of fish
5.9	5.6	119	0.75	2
6.4	6.2	130	0.94	4
6.9	6.8	143	1.67	3
7.4	—	—	—	—
7.9	7.8	165	2.53	9
8.4	8.2	173	2.78	8
8.9	8.7	183	3.12	35
9.4	9.1	192	3.76	22
9.9	9.6	202	4.57	7
10.4	10.1	213	5.12	10
10.9	10.8	228	6.67	3
11.4	11.2	237	7.88	6
11.9	11.7	246	8.61	7
12.4	12.1	256	10.25	6
12.9	12.7	267	10.95	5
13.4	13.2	278	12.35	5
13.9	13.6	286	12.38	2
14.4	—	—	—	—
14.9	14.5	306	14.75	1
14.9	9.6	201	5.00	135 ¹

¹ 13 taken in trap nets (Sandusky 76, Huron 28, Conneaut 5, Toledo 4), 17 in pound nets, Erie, Pa., 4 in gill nets and 1 in a bullnet in Vermilion, O. 63 were in 1927, 22 in 1928, 46 in 1929, and 4 in 1931.

56 feet, although we had collected random samples from approximately 5,616 bullnets and 11,520 shoal gill nets. Similarly, only a few units of the other gear fished caught mooneyes. Only 130 of the 1,493 trap nets taken 634 mooneyes (average 4.9), 16 of the pound nets had caught 17 specimens (average 0.9); and the several random samples of the two seines (Sandusky Bay) included 33 mooneyes (average 16.5). Our mooneyes had been distributed along the shore from Toledo, Ohio, to Erie, Pennsylvania.

Scales of 58 mooneyes were collected from various ports (Table 1). Age groups ranged from I to VII, and 53 percent of the fish belonged to age-group I. The average total lengths and weights of the different age groups varied from 8.4 to 13.1 inches and from 0.75 to 12.75 ounces (Table 2). Comparisons were made of the calculated standard lengths based on the anterior radii and lateral diameters of the scales. Because the annuli were not formed in the posterior area beyond the second or third summer the anterior-posterior measurements were not usable. Figure 1 shows that of the very few scales that revealed anterior circuli throughout the third year although the marginal part is relatively transparent.

The calculated standard and total lengths were greater when computed from diameters than from radii, although the differences were not significant after the second year. The

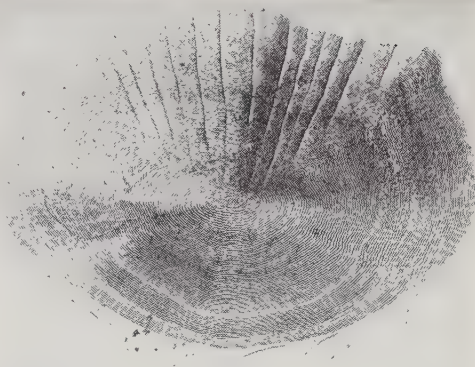


FIGURE 1.—Scale of Lake Erie mooneye, female, age-group II, two annuli, total length 8.8 inches, 2.75 ounces. September 15, 1927, Sandusky, Ohio. (Photographed by Clifford Tetzloff.)

results were due almost entirely to the increments of the first year when the two general averages differed 16 millimeters (0.8 inch). Throughout nearly all of the later years the increments computed from radii were greater but not enough to counteract the results of the first year. The grand average calculated lengths, especially those based on diameters, were decreased no more than 0.3 inch from the virtually completed actual lengths of the same age groups.

The length-weight relationship of 135 mooneyes collected in 1927–31 is shown in Table 3. They ranged from 5.6 to 14.5 inches total length and from 0.75 to 14.75 ounces. Twenty-six percent of these specimens ranged from 8.5 to 8.9 inches and averaged 8.7 inches in total length and 3.12 ounces in weight. Those that ranged from 8.5 to 9.4 inches constituted 42 percent and averaged 8.8 inches total length and 3.37 ounces in weight. The entire group averaged 9.6 inches and 5.0 ounces.

The sexual maturity of only 19 mooneyes was reported. Seven were males, nine females, and three immature unknown sexes. All nine of age-group I and the two of age-group II were immature. The remaining eight mooneyes were mature, five of them 3 years, and two, 5 years old. It appears that none of the immature specimens exceeded 8.8 inches and 3.25 ounces.

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Flavor and Aroma of Fish Taken from Four Fresh-Water Sources¹

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ABSTRACT

Taste-panel studies were conducted on fish taken from four fresh-water sources which included a cold deep lake, a shallow mixed water lake, and flowages above and below the entry of effluent from industrial plants. Fish were sampled at four seasons of the year. Taste-panel members rated the fish as to acceptability and described any unusual flavor or aroma noted. Statistical treatment of the data demonstrated that walleye (*Stizostedion vitreum vitreum*) taken from the source below the entry of effluent from industrial plants generally scored significantly lower than those from other sources. This trend was not as pronounced for carp (*Cyprinus carpio*) or for northern pike (*Esox lucius*). A predominance of undesirable descriptive terms was evident for the fish representing the lower-scoring source.

INTRODUCTION

Although in recent years much emphasis has been placed upon sensory testing of foods, there have been relatively few such studies on the flavor and aroma of fish. Much of the research which has been reported on fish has assessed the effects of storage, or the effects of the presence of effluent from industrial plants on the water sources from which fish were obtained.

It has been true in the case of many other foods, as approaches have been made to the study of the flavor and aroma of fish by applying chemical or sensory tests or by employing the two procedures concurrently. A comprehensive review of the literature pertaining to the chemical aspects of flavor and aroma of fish has been compiled by Bramstedt (1957) and translated by van Klaveren (1959). In the latter publication Obata and Yamanishi (1952) were credited with findings which suggested the possible role of nitrogenous substances, such as proteins, peptides, and amino acids, as the materials from which flavor and aroma of fish are developed. It was emphasized by Bramstedt (1957), however, that fats, organic acids, and their degradation products also make important contributions. The work of Obata and Yamanishi (1950) indicated that some specific compounds which

influenced flavor and aroma of fish were pyridine, piperidine and its acetate, and aldehydes and acids containing five carbon atoms. Unpleasant flavors were attributed to hydrogen sulphide and mercaptan compounds. Bramstedt suggested that unpleasant flavors in fish may be derived from the same agents as pleasant flavors with the difference in effect resulting from a variance in proportion of the compounds.

Wide interest has been shown in the influence which effluent discharged from industrial plants into natural waters may have upon flavor and aroma of fish taken from the waters. Studies have been conducted in Denmark, Russia, and Japan, as well as the United States (Demyanenko, 1933; Westfall and Ellis, 1940; Boëtius, 1954; Tamura, Itazawa, and Morita, 1954; Winston, 1959³). Tamura *et al.* (1954) classified the mode of action of industrial wastes as: (1) directly affecting flavor and aroma of fish; (2) causing toxic reactions in fish; and (3) indirectly influencing fish by depleting the oxygen supply in the water. Boëtius (1954), as well as Tamura and co-workers, stressed that the adverse effects of waste matter from industrial plants were dependent upon the concentration of the products in the water. Westfall and Ellis (1940) stated that undesirable flavors in fish subjected to paper-mill effluents might not be

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³ Winston, A. W., Jr. (1959) Test for odor imparted to the flesh of fish. Paper presented at the second seminar on Biological Problems in Water Pollution, Cincinnati, Ohio, April 20-24, 1959.

entirely due to the compounds as such, but also to the decomposition products of pulp fibers.

Demyanenko (1933) stated that certain compounds might cause undesirable changes in flavor and aroma even though the compounds were apparently tolerated by the fish. In attempting to determine the concentration of specific compounds which would bring about detectable changes in odor, Winston³ held fish under controlled conditions in aquaria. He found that specific levels could be established for diphenyloxyde and isopropyl benzene in the aquarium water which produced noticeable odor differences in the cooked fish.

In the research of Baeder and Tack (1945) emphasis was also placed on the application of sensory tests to fish subjected to differing environmental conditions. The flavor and aroma of wild brook trout were compared with that of hatchery-reared fish. Scoring by a panel of six judges indicated that the wild brook trout were considered superior in flavor and in aroma.

Sensory testing was employed in the present study. It was the purpose of this investigation to determine (1) whether flavor and aroma differences could be detected in selected species of fish taken from different water sources, and (2) whether flavor or aroma showed any relationship to length, weight, or sex of the fishes. The findings of this study will be of value to members of the fishing industry and industrial planners, as well as conservation departments and sportsmen.

These studies were financed in part by a grant from the Wisconsin State Committee on Water Pollution. Acknowledgment is made to the Wisconsin Conservation Department for providing the fish and to the Numerical Analysis Laboratory, University of Wisconsin, for making certain calculations.

EXPERIMENTAL PROCEDURE

Samples of fish for this project were taken from the various waters in the fall, winter, spring, and summer over a 2-year period. The water locations included a cold deep lake, a shallow mixed water lake, and flowages above and below the entry of effluent from industrial plants, most of which were paper mills. Hereinafter these water sources will be designated as shown in Table 1. Three species of fish, walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), and carp (*Cyprinus carpio*), were supplied by the Wisconsin

TABLE 1.—Water sources from which fish samples were taken

Water source	Abbreviation
Cold deep lake	C (control)
Shallow mixed water lake	M (mixed)
Flowage above the entry of effluent from industrial plants	A (above)
Flowage below the entry of effluent from industrial plants	B (below)

Conservation Department for this study. The extent of the testing program was limited by numbers of fish of suitable sizes and species which could be obtained from each source each season. Only the walleye was available for testing each of the four seasons for a 2-year period. The fish were packed in ice in labeled containers and transported by truck to Madison, Wisconsin. At the beginning of the study the fish were received in the Institution Management Laboratory of the University of Wisconsin. A group of laboratory workers determined length, weight, and sex of the fish. After fish were dressed, fillets were cut, wrapped in heavy-duty aluminum foil, identified, and placed in freezer storage (average temperature -17°F.). Later it was found more satisfactory to deliver fish to the local fish market where a skilled cutter worked with the laboratory personnel. Difficulties were countered at two of the water sources in northern Wisconsin made it necessary in some cases to clean fish prior to delivery. In these instances the fish were weighed, the sex determined at the place of catch, and the information attached to each fish. The transportation and subsequent handling was the same as for other samples.

A rating scale for flavor and aroma was used by the panel of staff and men and women students who served as judges for the sensory tests. The number of judges varied from ten to eight. It was not possible to retain the same taste-panel members throughout the entire study, but some of the members served through several seasons of testing, and the same judges were used throughout each series of tests.

The general nature of the problem under consideration was explained to the taste-panel members. They were informed that more than one species of fish were being tested and that fish were obtained from waters of different types. The specific water sources, the block upon which these sources were selected, and the order in which samples were tested were not known by the judges.

at least three late-afternoon tasting sessions, approximately $\frac{1}{2}$ hour in length, were held weekly during each series of evaluations. A specially designed room facilitated seating judges one behind the other at small shelves. Northeast daylight was used for the first series of tests. All later sessions were conducted in semi-darkness because it seemed that the lighting difference in color of the fish samples might influence the flavor judgments.

Prior to the collection of data for each of fall, winter, spring, and summer series of tests, four orientation sessions were conducted to familiarize the judges with the scoring instrument used, as well as test procedures and size of sample.

During the series of taste-panel tests, each sample was evaluated, in addition to an initial "warm-up" sample, two species of fish from various locations. Samples of one species of fish from as many sources as it was available were presented to a judge at one time. If a judge received one species of fish first on one day, it was the second served at the next testing. A brief discussion period followed the completion of the judging of all samples for each given day. Four replications for each source were completed in each season and are referred to in this paper as one series of tests. Considering the samples, judges first scored aroma and then flavor. A solution of lemon juice in water (2 tablespoons lemon juice in quart of water) at room temperature was applied for freshening the mouth between samples.

The working definitions of flavor and aroma as established at preliminary tasting sessions were: (A) The sensation experienced in sniffing, as opposed to ordinary breathing, was considered aroma or odor. These terms were used interchangeably. (B) Characteristics observed when food was eaten in the mouth were designated as flavor. Judges were instructed to disregard texture and appearance. Flavor was confined to impressions occurring during or immediately after mastication and swallowing.

A range of scores from one to eight was used by the judges in making their evaluations (Table 2). These values allowed judgments of flavors graded from unacceptable to excellent and highly acceptable. In addition to rating the flavor and aroma, a word description of any outstanding flavor was recorded by the judge.

The terms, freely chosen by judges in describing the fish samples, were summarized

TABLE 2.—Range of scores used by taste-panel members

Numerical score	Corresponding evaluation of acceptability
8	Excellent
7	Very good
6	Good
5	Fairly good
4	Just acceptable
3	Not quite acceptable
2	Very poor—inedible
1	Extremely poor—repulsive

by preparing a tally of the number of times various descriptions were applied. The terms were grouped according to species of fish and source from which the fish were taken. By this means it was possible to discover which words were used most frequently for a particular species of fish taken from a specific location. The appearance of the same descriptive term three or more times in a series was arbitrarily set as the criterion for classification in the category of frequently used terms.

Preliminary work on methods of preparing the fish led to the adoption of a standard procedure which allowed maximum uniformity from sample to sample and from time to time. The frozen fish was cut into cubes (approximately 1 inch) prior to grinding in a heavy-duty blender. Three or four cubes were ground at one time for approximately 7 seconds. Twenty-gram aliquots of the uniformly ground fish were placed in 30-milliliter beakers, each of which was covered with heavy-duty aluminum foil. A roasting pan served as a rack for the samples of fish which were baked at an oven temperature of 325°F. until an internal temperature of 160°F. was reached.

Taste-panel members were considered as a random sample of judges, and statistical treatment was applied to the scores for flavor and aroma of the various fishes. Because the number of judges varied from season to season, average scores were used in analyzing the data. Since more exact treatment would have affected only those findings which were borderline, this procedure was considered justifiable.

Analyses of variance for flavor and for aroma were completed for each species of fish for each season and over all seasons in which it was tested. Interaction of judges times source was used to test significance among sources. Differences among sources within species were compared by Duncan's (1955) new multiple range test. Correlation coefficients were calculated in order to determine

TABLE 3.—Mean scores¹ for flavor evaluations for three species of fishes² taken from four water sources

[Where exponent letters differ within season, mean scores for sources differ significantly]

Season	Walleye				Northern pike				Carp		
	C	Water A	source B	M	C	Water A	source B	M	C	Water source B	M
1957-58											
Fall	5.5 ^{ab}	4.8 ^{bc}	4.4 ^c	5.6 ^a	5.2 ^a	5.0 ^a	4.6 ^a	4.5 ^a	4.1 ^a	2.6 ^c	3.3 ^b
Winter	4.8 ^a	5.3 ^a	4.5 ^a	5.2 ^a	—	—	—	—	—	—	—
Spring	5.0 ^a	5.3 ^a	3.3 ^b	5.3 ^a	4.3 ^b	4.9 ^a	3.1 ^c	5.2 ^a	3.5 ^a	2.9 ^b	2.4 ^b
Summer	5.4 ^a	5.2 ^a	3.2 ^b	6.2 ^a	—	4.4 ^a	4.3 ^a	3.7 ^a	4.1 ^a	3.5 ^a	2.3 ^b
1958-59											
Fall	4.8 ^a	4.9 ^a	3.2 ^b	5.6 ^a	4.2 ^b	3.7 ^b	4.1 ^b	5.0 ^a	3.5 ^a	—	2.0 ^b
Winter	4.5 ^a	5.0 ^a	3.7 ^b	5.0 ^a	—	—	—	—	—	—	—
Spring	4.2 ^b	5.2 ^a	2.2 ^c	4.8 ^{ab}	—	5.4 ^a	2.8 ^b	4.8 ^a	2.8 ^{ab}	2.3 ^b	3.1 ^a
Summer	6.5 ^a	6.0 ^{ab}	3.9 ^c	5.6 ^b	—	5.5 ^a	4.2 ^b	5.9 ^a	5.3 ^a	2.6 ^b	5.1 ^a
Average, all seasons	5.1 ^a	5.2 ^a	3.5 ^b	5.4 ^a	4.6 ^a	4.8 ^a	3.8 ^b	4.8 ^a	3.9 ^a	2.8 ^b	3.0 ^b

¹ Mean scores for the four replications included in the series. (Three replications only for northern pike, summer 1957-58, source B.)² Northern pike and carp were not available from all sources in all seasons.

whether or not weight or length showed any linear relationship to flavor. Effect of sex upon flavor and aroma was also tested. Unless otherwise stated, values were considered significant at the 5 percent level.

RESULTS AND DISCUSSION

The findings from this study of three species of fishes taken from different fresh-water sources appeared to indicate certain trends which shed some light on the relationship between conditions in the water source and the flavor and aroma of the fish taken from the waters. Differences in flavor and aroma were found for fishes according to the water source from which they were taken. In addition, descriptive terms frequently used by the judges in characterizing the flavor and aroma of the fish appeared to show tendencies which were associated with particular water sources. In general, significantly lower scores for flavor and aroma were coupled with a predominance

of unfavorable descriptive terms. Although species comparisons were not included in objectives of this study, the data permitted some observations. For example, relatively low scores for both flavor and aroma and desirable qualities were attributed to carp regardless of the source from which it was taken.

Mean scores for flavor for the four replications included in each series of tests are shown in Table 3. The differences in average responses between the sources appeared to be fairly consistent for the various species from season to season within the year and from year to year. There was a tendency toward higher scores for flavor for the summer 1959 samples. Any trend toward higher or lower ratings for fish samples for any one season was not evident in the evaluations of aroma (Table 4).

Application of Duncan's new multiple range test showed a trend toward lower scores for

TABLE 4.—Mean scores¹ for aroma evaluations for three species of fishes² taken from four water sources

[Where exponent letters differ within season, mean scores for sources differ significantly]

Season	Walleye				Northern pike				Carp		
	C	Water A	source B	M	C	Water A	source B	M	C	Water source B	M
1957-58											
Fall	5.7 ^a	5.3 ^a	4.3 ^b	5.6 ^a	5.0 ^a	5.1 ^a	4.5 ^a	4.9 ^a	4.6 ^a	3.4 ^b	3.9 ^b
Winter	4.9 ^b	5.4 ^a	4.5 ^b	4.9 ^b	—	—	—	—	—	—	—
Spring	4.6 ^a	5.0 ^a	3.7 ^b	5.1 ^a	4.1 ^b	4.7 ^a	3.3 ^c	5.0 ^a	3.4 ^a	3.0 ^a	2.9 ^a
Summer	5.8 ^a	5.7 ^a	3.8 ^b	6.3 ^a	—	4.9 ^a	4.7 ^a	4.0 ^a	4.6 ^a	3.6 ^b	2.4 ^c
1958-59											
Fall	4.5 ^a	4.7 ^a	3.2 ^b	5.1 ^a	4.3 ^a	4.4 ^a	4.3 ^a	5.0 ^a	3.8 ^a	—	2.7 ^b
Winter	3.8 ^{bc}	4.7 ^{ab}	3.6 ^c	5.1 ^a	—	—	—	—	—	—	—
Spring	4.4 ^a	5.1 ^a	2.2 ^b	4.7 ^a	—	5.0 ^a	3.2 ^b	4.8 ^a	3.9 ^a	2.4 ^b	3.6 ^a
Summer	5.9 ^a	5.7 ^{ab}	4.1 ^c	5.4 ^b	—	5.2 ^a	4.2 ^b	5.8 ^a	5.2 ^a	3.2 ^b	5.3 ^a
Average, all seasons	5.0 ^b	5.2 ^{ab}	3.7 ^c	5.3 ^a	4.5 ^b	4.9 ^a	3.9 ^c	4.9 ^a	4.3 ^a	3.1 ^c	3.5 ^b

^{1,2} See footnotes 1 and 2 of Table 3.

or and aroma in fish taken from the location B, below the entry of industrial effluent including that from paper mills. Over all seasons the fishes taken from source B were rated significantly lower in aroma than those from other sources. This was also true for flavor in the exception of carp from sources B and M for which no difference was indicated.

Lower mean scores were obtained for walleye from source B in each of the eight seasons. The scores were significantly lower in flavor in six, and in aroma in seven seasons. In one winter, however, differences were indicated in neither flavor nor aroma among walleye from sources B, C, and M.

Among the sources and seasons for which northern pike were tested, scores for both flavor and aroma were lower for fish from source B than from other locations in three seasons. No significant differences were observed among the northern pike from the various sources in flavor in two, and in aroma in three seasons. In one fall, higher scores were obtained for northern pike from source M than from sources C, A, and B, which did not differ from each other.

In flavor, carp from source B did not differ from source M in one series, nor from source C in two series of tests. In one season, lower scores for both flavor and aroma were demonstrated for carp from source B than from sources C and M. For the latter two the mean scores showed no difference. In the fall of 1947, carp from all sources differed from each other in flavor. Fish from sources B and C were rated lowest and highest, respectively. In aroma, however, no difference was indicated for carp taken from locations B and M. In spring no difference was detected in aroma among the sources.

Selection of terms for description of flavor and aroma was left entirely to the discretion of the judges. Considerable difficulty was encountered in attempting to describe adequately the flavor of good fish. It was agreed, however, that it should be mild, but not flat, and slightly sweet. It was felt that no other terms should appropriately be included in a general characterization. The slightly spicy flavor referred to by Bramstedt (1957) was not indicated. Since the taste-panel members were familiar with the origin of the samples, it would seem that the terms frequently recorded as descriptive terms might be considered as unbiased.

The words, mild, sweet, and flat, were prominent among descriptions of both wal-

leye and northern pike from locations A, C, and M. In contrast, the words, bitter and woody, were used by judges to describe these fishes from source B. Carp, on the other hand, was not characterized by any one impression from one source. The terms, fishy and musty, were applied to this species regardless of location from which it was taken.

Correlation coefficients were determined between certain characteristics, namely weight and length of the fishes and the flavor and aroma. For each comparison two correlations, called between and within, were calculated. The between correlation measures the association based upon the mean of each source for each season, whereas the within correlation is calculated from the individual replicate values within a season source and estimates the average relationship within a source for a season.

In the case of walleye, all correlation coefficients for the variables of weight and length were negative, but none was significant. All correlation coefficients for northern pike were positive and the within correlation for aroma and weight was significant. These latter correlations indicate a slight tendency for heavier fish within a source for a season to be scored higher for aroma than were lighter fish. For carp, between correlations were all negative and significant, whereas none of the within correlations was significant. Thus the season locations with longer and with heavier carp showed tendencies toward lower scores for flavor and aroma.

No differences in flavor and aroma were found between sexes for all of the species of fish. Mean scores for flavor for male and female walleye were 4.6 and 4.9, respectively. This represented as great a variation for mean scores between the sexes as was shown for any species for ratings for either flavor or aroma. From the above data it might be inferred that for the fishes included in this study, little influence upon flavor or aroma was exerted by weight or length or sex of the fishes.

IMPLICATIONS

The studies of Westfall and Ellis (1940) and Cole (1935) indicated that the discharge of effluent from paper mills into the natural water was associated with undesirable flavor in fish taken from the water. The findings in the present study are in agreement with these earlier investigations.

The Wisconsin State Committee on Water

Pollution conducted chemical analyses on samples of water taken from locations where fish for the study were obtained. A substantial difference in sulphate content among the various waters was found, with source B showing much higher amounts than other sources. It would be erroneous to state, however, that the effluent from paper mills was responsible for this difference in sulphate content of the waters; and that this, in turn, was responsible for the trend toward lower ratings for the fishes taken from this location. Neither was evidence to discount this possibility obtained. The presence or absence of effluent from paper mills was one major point of difference among the locations. There was also a measurable difference in the flavor of fish taken from such water. It is possible that other differences may have existed and exerted an influence on the observed differences in flavor and aroma.

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Catch Curves and Mortality Rates¹

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ABSTRACT

The assumptions necessary to obtain a valid estimate of survival rate from a single catch curve are discussed. An example of the best estimate of survival rate and its variance is worked out for the case that age is known exactly for the entire sample. A test for validity of the model is illustrated. Methods of estimating the survival rate are also given when some age groups are combined, when an age-length key is used, and when only a segment of the catch curve is usable. A table is provided to facilitate the estimation in this last case.

INTRODUCTION

The analysis of a catch curve, or the age-frequency distribution of the catch, to obtain information on the vital statistics of a fish population goes back at least to Edser (1908), who published catch curves for plaice of the North Sea. The earlier users worked with age indirectly, using some correlated variable such as body length to separate the catch approximately into age groups. Today, however, improved aging techniques such as scale analysis make it possible to work directly with age in most studies.

When plotted graphically, the age-frequency distribution in a population typically presents a staircase appearance, descending with increasing age, and with the height of the steps gradually decreasing. The basic idea underlying catch-curve analysis is that the drop in frequency from one age group to the next reflects the combined effect of mortality and difference in initial year-class strength for two age groups. The amount and kind of information which can be extracted from a catch curve, however, depends upon the amount and kind of information which the investigator can put into the underlying models of the population and the sampling process, or depends, in other words, upon the set of simplifying assumptions which can be reasonably made concerning the population and the sampling process. The user may, for example, acknowledge that his sampling gear is selective against younger fish, but may consider it reasonable to assume that beyond the minimum age all fish are equally vul-

nerable to the gear employed. Information concerning the relative year-class strengths and survival rates may be available from other sources, either direct information from previous studies on this same population or indirectly from the results of studies on similar populations.

If no simplifying assumptions concerning the population can be made or if year classes must be acknowledged to vary in strength and survival rates to vary from year class to year class and age to age, then the age-frequency distribution in the catch of a single season provides no identifiable information whatsoever regarding these unknown population parameters. In order to separate the effects of mortality from the effects of variable year-class strength, it becomes necessary to obtain catches over a series of years, and either provide that the expected average catch per unit of effort remains each year in constant proportion to total abundance, or to supplement—or even replace—the catch-curve analysis with a tag-recapture program.

The theory of catch-curve analysis, however, should logically begin with the simpler problem of a single catch curve and a simplified population and sampling model. The present paper will be concerned exclusively with this simple and classical problem in which year-class strength and annual survival rates are assumed to be constant, at least over a limited range of age groups, in which case the problem reduces to examination of methods of estimating the constant but unknown annual survival rate. Included in our discussion, however, are several methods for testing these basic, simplifying assumptions.

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METHODS OF ANALYSIS WHEN AGE IS KNOWN
FOR ENTIRE SAMPLE

Chapman and Robson (1960) have shown that unbiased estimates of annual survival rate may be derived from the catch curve for a single season if the assumptions of constant year-class strength and survival rate hold true and if all fish beyond some minimum age are equally vulnerable to the sampling gear. Furthermore, among the many possible unbiased estimators which exist in this case, there is one which is uniquely best in the sense that it is subject to the smallest amount of sampling error. To illustrate the form of this and other analytic procedures we shall employ the age-frequency distribution in a sample of 243 rock bass of age VI⁺ and older, trap-netted from Cayuga Lake, New York, during a single summer season.² For the present purposes, VI⁺ was arbitrarily chosen to represent the youngest age group fully vulnerable to trap-netting. The age composition of this catch is shown in the age-frequency table below, with age VI⁺ coded back to 0:

Age	Coded age	Number in catch
VI ⁺	0	$N_0 = 118$
VII ⁺	1	$N_1 = 73$
VIII ⁺	2	$N_2 = 36$
IX ⁺	3	$N_3 = 14$
X ⁺	4	$N_4 = 1$
XI ⁺	5	$N_5 = 1$
Total sample size		$n = 243$

The best estimate of the assumed constant annual survival rate is based upon the total or mean coded age in the sample. If T denotes total and n denotes sample size, then here

$$\begin{aligned} T &= N_1 + 2N_2 + 3N_3 + \dots \\ &= 73 + 2(36) + 3(14) + 4(1) + 5(1) \\ &= 196 \end{aligned}$$

and

$$\begin{aligned} n &= N_0 + N_1 + N_2 + \dots \\ &= 118 + 73 + 36 + 14 + 1 + 1 \\ &= 243 \end{aligned}$$

The best estimate of survival rate is then computed from the formula

$$\begin{aligned} \text{Annual survival rate estimate} &= \frac{T}{n + T - 1} \\ &= \frac{196}{196 + 243 - 1} \\ &= .4475 \end{aligned}$$

We repeat that in this estimation procedure the initial age used in the estimation procedure must be coded as age zero.

If the true annual survival rate in the population is s , then among samples of size n the average value of this estimator will be exactly s , and the variance about this average value will be

$$\text{Variance of estimate} = \frac{s(1-s)^2}{n}$$

Since the variance of the estimate depends upon the unknown true survival rate s the variance, likewise, is unknown and must be estimated from the sample, and is therefore also subject to sampling error. The best estimate of the variance, in the sense of being unbiased and subject to the smallest possible sampling error, is given by

$$\begin{aligned} \text{Estimate of variance} &= \frac{T}{n + T - 1} \left(\frac{T}{n + T - 1} - \frac{T - 1}{n + T - 1} \right) \\ &= \frac{196}{438} \left(\frac{196}{438} - \frac{195}{437} \right) \\ &= .000566 \end{aligned}$$

The standard error, or square root of variance, is therefore estimated by

$$\text{Standard error} = \sqrt{.000566} = .0238$$

Since the sampling distribution of the survival rate estimate approaches the normal distribution as sample size gets large, approximately 95 percent confidence intervals on the survival rate are given by

$$\begin{aligned} \text{survival rate} - 2(\text{standard error}) &< s < \\ \text{survival rate} + 2(\text{standard error}) \end{aligned}$$

or

$$\begin{aligned} .4475 - 2(.0238) &= .40 < s < .50 \\ &= .4475 + 2(.0238) \end{aligned}$$

Thus, one could state with (95 percent) confidence that if year-class size and survival rates are actually constant in this rock bass population, then the true annual survival rate falls somewhere between 40 percent and 50 percent, with the best point estimate being 45 percent.

²Data provided by D. A. Webster of Cornell University.

Other estimates exist which are unbiased under simplifying assumptions of the model are true, and differences between alternative unbiased estimates may in fact be used as criteria to test the validity of the simplified model. One such alternative estimate especially suited to this purpose is Heincke's (1933) estimate of survival rate, $(n - N_0)/n$. This is essentially the same as Jackson's (1939) estimate $(n - N_0)/(n - N_k)$, where N_k is the number of fish in the oldest age group occurring in the sample and is usually a small number relative to the total sample size n and the number N_0 occurring in the youngest age group. Insofar as Heincke's and Jackson's estimates do differ, Heincke's is the better in this case, since it is unbiased and subject to the smaller sampling error. For the example used here, Heincke's estimate becomes

$$\frac{n - N_0}{n} = \frac{243 - 118}{243} = \frac{125}{243} = .5144.$$

When a discrepancy arises between Heincke's estimate and the best estimate, it may be attributed directly to a discrepancy in the age-group frequency relative to the frequency in the older age groups. In the present example, Heincke's estimate exceeds the value .5144 obtained for the best estimate, implying a deficit in the 0 group relative to the older age groups. The test of whether this observed discrepancy may be attributed to sampling error or must be considered as real takes the form of a chi-square test:

$$\begin{aligned} \text{chi square} &= \frac{(\text{Best est.} - \text{Heincke's est.})^2}{\text{with 1 d.f.} \quad \frac{T(T-1)(n-1)}{n(n+T-1)^2(n+T-2)}} \\ &= \frac{(.4475 - .5144)^2}{\frac{196(195)(242)}{243(438)^2(437)}} \\ &= 9.858 > 3.841 \end{aligned}$$

Since the chi-square values in excess of 3.841 require only 5 percent of the time when the discrepancies are due solely to sampling errors, we must in this case reject the hypothesis that the observed discrepancy is a result of sampling error. Our conclusion must therefore be that the fault lies with the basic model which implied that these estimates should differ only by sampling error. The fault may lie in the assumption of constant year-class size or in the assumption of constant survival rate

or in the assumption of equal vulnerability of all age groups to the sampling gear. The chi-square test cannot discriminate between the possible causes of the failure of the model, but merely establishes whether or not reasonable agreement exists between the observed frequency in age-group 0 and the frequency expected on the basis of the data in the older age groups.

An exactly analogous test procedure may be applied to age-group I simply by eliminating age-group 0 from the data, recoding, and then applying the above formulae to the reduced data. Upon eliminating age 0 and then recoding we obtain for this example:

Age	Recoded age	Number in catch
VII+	0	73
VIII+	1	36
IX+	2	14
X+	3	1
XI+	4	1

Total sample size $n = 125$

The new total T then becomes

$$T = 36 + 2(14) + 3(1) + 4(1) = 71$$

and with $n = 125$ the best estimate of survival rate is

$$\frac{T}{n + T - 1} = \frac{71}{125 + 71 - 1} = .3641.$$

The new N_0 is 73, so Heincke's estimate for these reduced data is

$$\frac{n - N_0}{n} = \frac{125 - 73}{125} = .4160.$$

Again, the discrepancy between the two estimates is in the direction which implies a deficiency in the youngest age group, and chi-square value

$$\begin{aligned} &= \frac{(\text{Best est.} - \text{Heincke's est.})^2}{\frac{T(T-1)(n-1)/n(n+T-1)^2(n+T-2)}{71(70)(124)/125(195)^2(194)}} = \\ &= 4.032 \end{aligned}$$

shows this deficiency in age VII⁺ to be significant.

This process may be continued by starting the age-frequency table with age VIII⁺ as the 0-group, and in this example the resulting chi-square value is non-significant. With rock bass, selectivity of the trap net for larger and

therefore older fish cannot be ruled out as a possible explanation of the observed deficiencies in ages even as great as VI⁺ and VII⁺.

METHODS OF ANALYSIS WHEN SOME AGE GROUPS ARE COMBINED

Thus far we have assumed that when the simplified model does hold true, the only error in the estimate is the random error associated with the sampling process. In practice another source of error variation is the process of measuring age. Two independent age determinations on the same fish specimen do not always yield the same result. With such commonly used procedures as scale or otolith reading the difficulty of age determination and the frequency of aging errors increase with the age of the fish. One way to alleviate this difficulty and at the same time eliminate the majority of the aging errors is simply to attempt exact aging only for the younger age groups and combine all of the remaining age groups. This technique clearly sacrifices some of the potential information contained in the sample, but on the other hand, the greater ease of operation may permit the use of larger samples to compensate for this loss. It would seem worth while, therefore, to investigate the estimation problem and the loss in statistical efficiency associated with this technique.

In general, if fish up through K years of age are all aged exactly and all fish $K + 1$ years old or older are grouped together, then the tabulated age-frequency distribution will take the form:

Coded age	Number in catch
0	N_0
1	N_1
2	N_2
.	
.	
K	N_K
$K + 1$ or older	m
Total sample size n	

The best (maximum likelihood) estimate of annual survival rate in this case depends on the total T and the sample size n

$$T = N_1 + 2N_2 + 3N_3 + \dots + KN_K + m(K + 1)$$

$$n = N_0 + N_1 + N_2 + \dots + N_K + m$$

and takes the form

$$\text{Annual survival rate estimate} = \frac{T}{n - m + T}.$$

The variance of this estimate, under the assumption that no errors are committed in this modified age-classification technique,

$$\text{Variance of estimate} = \frac{s(1-s)^2}{n(1-s^{K+1})}$$

where s is again the true survival rate in the population being sampled. The efficiency of this technique relative to aging all fish exactly is therefore $100(1-s^{K+1})$ percent; in other words, to obtain the same accuracy by this method as is obtained by aging all fish exactly, the present method would require $100/(1-s^{K+1})$ fish for every 100 fish used in the old method. Table 1 shows the numerical value of this relation for several values of s and K , and it is apparent that with survival rates in the neighborhood of .50, which commonly occur in practice, little would be gained by attempting exact aging on more than the first two or three groups if this method of estimation is to be employed.

The numerical computation of this estimate of survival rate for the rock bass data has already been illustrated for the case $K = 2$ since in this case the estimate reduces to the unbiased estimate proposed by Heinicke. For another example, if all rock bass of age II and older were grouped together,

Age	Coded age	Number in catch
VI+	0	118
VII+	1	73
VIII+	2	36
IX+ and older	3 and older	16
Total sample size		243

the estimate of survival rate would be

$$T = 73 + 2(36) + 3(16) = 193$$

$$n = 118 + 73 + 36 + 16 = 243$$

$$m = 16$$

$$\frac{T}{n - m + T} = \frac{193}{243 - 16 + 193} = \frac{193}{420} = .46$$

compared to the value .45 obtained when all age groups were held separate. The variance of the estimate would, in turn, be estimated by applying this estimate of s to the variance formula $s(1-s)^2/n(1-s^3)$

$$\frac{.46(1-.46)^2}{243[1-(.46)^3]} = .000612.$$

Fig. 1.—Sample size required to obtain precision equal to that of a sample of 100 in which all fish aged exactly

Grouped together	True annual survival rate in the population		
	.25	.50	.75
and older	133	200	400
and older	107	133	228
and older	101	114	173
and older	100	107	146
and older	100	103	132
and older	100	101	122
...	...	...	...
aged exactly	100	100	100

expected, this is only slightly larger than value .000566 obtained earlier for the case where all fish were aged exactly.

METHOD OF ANALYSIS WHEN AGE-LENGTH KEY IS USED

Where large samples of fish are available in the sampling program of a commercial fishery, or where age determinations are tedious, it may be impractical or inefficient to age all fish sampled for age. If age and length are correlated, it is more efficient to use an age-length key, *i.e.*, to stratify the whole fish sample by lengths and make an age determination for a subsample within each length.

Such a stratified sampling procedure makes use of two sample sizes: n , the total sample size for lengths; and the subsample n' , read for age as well. This raises a question as to what sample size is appropriate in the formulae given for the estimate of survival rate and the variance of this estimate. In fact, modifications must be made.

From the stratified subsample is obtained an estimate, which we denote by T^* , of the true coded ages T of the whole sample. The procedure of estimating a stratified sample is shown by Cochran (1953, page 70), and if T^* is substituted in the formula to estimate survival rate, the result is biased. In fact, the variance estimate is too small. The modified formulae are:

$$\text{Survival} = \frac{T^*}{n + T^* - 1} + \frac{(n-1) \text{ var } T^*}{(n + T^* - 1)(n + T^* - 2)(n + T^* - 3)}$$

and the variance of this estimate is

$$\frac{s(1-s)^2}{n} + \frac{(1-s)^4}{(n-1)^2} \text{ var } T^*$$

Here $\text{var } T^*$ is the variance within the stratified sample. The corrections given are first-order corrections valid for large n , n' (in which case the factors -1 , -2 , -3 in the formulae given are quite insignificant).

The procedure is illustrated by a worked example on data kindly provided by W. Hardman of the International Pacific Halibut Commission. Using the results of calculations given in Table 2, the estimate of annual survival rate is

$$\frac{5659.67}{1612 + 5659.67 - 1} + \frac{(1611)(13,704.55)}{(7270.67)(7269.67)(7268.67)} = 0.7785$$

The bias correction here is quite negligible while the variance of survival rate estimate

$$= \frac{(.7785)(1 - .7785)^2}{1612} + \frac{(1 - .78)^4}{(1611)^2} (13,704.55) = .000024 + .000012 = .000036.$$

Since the subsample is an appreciable fraction of the whole sample, the finite population correction is used in calculating the variance of T^* . The approximate 95 percent confidence interval for the survival rate is $.779 \pm 2(.006)$ or $(.767, .791)$, provided of course the data satisfy the assumptions noted in the introduction.

The estimated optimum allocation of effort between length sampling and age sampling, *i.e.*, the relative sizes of n , n' are easily determined from such data, provided the subsampling be restricted to proportional allocation. The simplest procedure is to calculate the variance of T^* without the finite population correction and then put the indicated components of variance on a per-unit basis, *i.e.*, by multiplying them by n and n' respectively. Denote these by S_L^2 and $S_{A'}^2$, the components of variance due to the length and age samples, *i.e.*,

$$S_L^2 = s(1-s)^2$$

$$S_{A'}^2 = n' \frac{(1-s)^4}{(n-1)^2} \sum \frac{S_i^2 n_i}{n_i^2}$$

If the relative cost of an age determination to a length reading is C , then the indicated

TABLE 2.—Example of estimation of annual survival rate from halibut stratified by length and subsampling for age determinations

Length stratum (cm)	Number in stratum	Number in stratum subsampled for age determination	Total coded age of stratum subsample	Variance about mean of stratum subsample	$\frac{n_i}{n_i'}(T_i)$	$S_i^2 n_i^2 \left(1 - \frac{n_i}{n_i'}\right)$
	n_i	n_i'	T_i	S_i^2		n_i'
≤ 95	25	13	28	3.31	53.75	76.38
100	37	18	42	6.59	86.21	257.38
105	79	40	57	3.79	112.97	291.92
110	146	75	90	3.51	175.20	485.13
115	204	103	191	5.95	377.40	1,190.23
120	259	132	296	7.15	580.16	1,781.70
125	224	103	291	7.89	633.92	2,076.22
130	177	81	389	4.74	849.60	994.35
135	163	74	340	8.76	748.17	1,717.32
140	116	61	363	12.78	690.20	1,336.66
145	87	41	266	16.01	564.63	1,562.73
150	37	20	168	20.46	310.80	643.47
155	26	16	107	21.83	173.94	354.74
≥ 160	32	13	123	20.02	302.72	936.32
Totals	1612	790			5,659.67	13,704.55
	(= n)	(= n')			(= T*)	(= variance T*)

optimum fraction, *f*, of the length sample to be aged

$$f_{\text{optimum}} = \frac{S_A}{\sqrt{S_L^2 - S_A^2}} \cdot \frac{1}{\sqrt{C}}$$

If $S_A^2 \geq S_L^2$ then 100 percent subsampling is indicated. For the halibut data

$$S_L^2 = .038195$$
$$S_A^2 = .019244$$

so that

$$f_{\text{optimum}} = (1.0077)/\sqrt{C}$$

For *C* = 10 this works out to a sampling ratio of one age reading to each three length readings.

It should be noted that the age-length relationship may be utilized in another form, viz., the total age in the complete sample can be estimated from a regression estimate. The formulae given for the estimate of survival rate and its variance are still valid. In this case variance *T** is that determined from the regression estimate, as may be found in Cochran (1953, p. 145).

METHODS OF ANALYZING A SEGMENT OF CATCH CURVE

Circumstances frequently arise which make it necessary to truncate the catch curve on the right as well as the left. The sampling gear, for example, may be effective only for a limited range of fish size and therefore age, so that different gear is used for each of several size classes, and these different pieces of

gear may operate at different levels of efficiency; or the exploitation of the fishery may be differentially selective for different age classes, thus precluding a constant survival rate. Such circumstances lead to a partitioning of the catch curve into segments and separate analysis on each segment, so we now consider now methods of analyzing a segment of a catch curve.

Following the notation of the preceding sections, we may denote the age groups within a segment as ranging from 0 to *K* on the coded scale:

Coded age	Number in catch
0	N_0
1	N_1
2	N_2
.	.
.	.
$\dot{K}$	N_K
Total number <i>n</i>	

The annual survival rate, which is assumed to be constant for this set of age groups in the population, is then estimated as the solution to the equation

$$\frac{T_K}{n} = \bar{x}_K = \frac{s}{1-s} - (K+1) \frac{s^{K+1}}{1-s^{K+1}}$$

where

$$T_K = N_1 + 2N_2 + 3N_3 + \dots + KN_K$$
$$n = N_0 + N_1 + N_2 + \dots + N_K$$

and $\bar{x}_K = T_K/n$ is the average coded age of this segment of the sample; for *K* = 1, *i*

3.—Table for estimation of annual survival rate from the coded mean age of a segment of the catch
ve¹

K = 2 Three classes	K = 3 Four classes	K = 4 Five classes	K = 5 Six classes	K = 6 Seven classes	K = 7 Eight classes	K = 8 Nine classes
.0101	.0110	.0110	.0110	.0110	.0110	.0110
.0204	.0204	.0204	.0204	.0204	.0204	.0204
.0308	.0309	.0309	.0309	.0309	.0309	.0309
.0415	.0416	.0416	.0416	.0416	.0416	.0416
.0523	.0526	.0527	.0527	.0527	.0527	.0527
.0632	.0638	.0638	.0638	.0638	.0638	.0638
.0742	.0742	.0752	.0752	.0752	.0752	.0752
.0854	.0868	.0869	.0869	.0869	.0869	.0869
.0967	.0986	.0989	.0989	.0989	.0989	.0989
.1081	.1107	.1111	.1111	.1111	.1111	.1111
.1196	.1230	.1235	.1236	.1236	.1236	.1236
.1312	.1355	.1363	.1364	.1364	.1364	.1364
.1428	.1483	.1493	.1494	.1495	.1495	.1495
.1545	.1612	.1625	.1627	.1628	.1628	.1628
.1663	.1744	.1761	.1764	.1765	.1765	.1765
.1781	.1879	.1900	.1904	.1905	.1905	.1905
.1900	.2015	.2041	.2047	.2047	.2047	.2047
.2019	.2153	.2186	.2193	.2195	.2195	.2195
.2138	.2294	.2333	.2343	.2345	.2346	.2346
.2258	.2436	.2484	.2496	.2499	.2499	.2499
.2378	.2580	.2638	.2653	.2657	.2658	.2658
.2498	.2727	.2795	.2814	.2818	.2819	.2819
.2618	.2875	.2955	.2978	.2985	.2986	.2987
.2737	.3025	.3118	.3147	.3155	.3158	.3158
.2857	.3177	.3285	.3319	.3329	.3332	.3333
.2977	.3330	.3454	.3495	.3508	.3512	.3513
.3096	.3485	.3627	.3675	.3691	.3696	.3698
.3216	.3641	.3803	.3860	.3879	.3886	.3888
.3335	.3800	.3982	.4049	.4072	.4080	.4083
.3453	.3959	.4164	.4242	.4270	.4281	.4284
.3572	.4120	.4349	.4439	.4474	.4486	.4491
.3690	.4282	.4538	.4642	.4682	.4698	.4704
.3807	.4445	.4729	.4848	.4895	.4914	.4921
.3924	.4610	.4923	.5058	.5114	.5137	.5145
.4041	.4775	.5121	.5274	.5340	.5367	.5377
.4157	.4942	.5321	.5494	.5570	.5603	.5616
.4272	.5109	.5524	.5718	.5806	.5845	.5861
.4387	.5277	.5730	.5948	.6049	.6094	.6114
.4502	.5446	.5938	.6181	.6297	.6350	.6374
.4615	.5616	.6149	.6420	.6552	.6614	.6643
.4728	.5786	.6363	.6663	.6813	.6885	.6920
.4841	.5957	.6579	.6910	.7080	.7164	.7205
.4953	.6128	.6798	.7162	.7353	.7450	.7499
.5064	.6299	.7019	.7418	.7633	.7745	.7801
.5174	.6471	.7242	.7679	.7919	.8047	.8114
.5284	.6644	.7467	.7945	.8212	.8358	.8435
.5392	.6816	.7694	.8214	.8512	.8677	.8767
.5500	.6988	.7923	.8488	.8817	.9005	.9109
.5608	.7161	.8154	.8766	.9130	.9341	.9461
.5714	.7333	.8387	.9048	.9449	.9686	.9824
.5820	.7506	.8621	.9333	.9774	1.0041	1.0198
.5925	.7678	.8857	.9623	1.0106	1.0403	1.0583
.6029	.7850	.9094	.9917	1.0445	1.0775	1.0978
.6132	.8022	.9333	1.0214	1.0789	1.1157	1.1387
.6235	.8193	.9573	1.0514	1.1140	1.1547	1.1806
.6336	.8365	.9813	1.0818	1.1497	1.1946	1.2237
.6437	.8535	1.0055	1.1125	1.1860	1.2354	1.2681
.6537	.8705	1.0297	1.1435	1.2229	1.2772	1.3136
.6636	.8875	1.0540	1.1748	1.2604	1.3198	1.3604
.6735	.9044	1.0784	1.2064	1.2984	1.3634	1.4084
.6832	.9213	1.1028	1.2382	1.3370	1.4077	1.4576
.6929	.9380	1.1273	1.2702	1.3761	1.4530	1.5081
.7025	.9548	1.1518	1.3025	1.4157	1.4991	1.5598
.7119	.9714	1.1763	1.3350	1.4557	1.5461	1.6127
.7214	.9880	1.2009	1.3677	1.4963	1.5938	1.6668
.7307	1.0044	1.2254	1.4006	1.5373	1.6423	1.7220
.7399	1.0208	1.2499	1.4336	1.5787	1.6917	1.7786
.7491	1.0371	1.2743	1.4667	1.6205	1.7417	1.8362
.7581	1.0534	1.2988	1.5000	1.6626	1.7925	1.8950
.7671	1.0695	1.3232	1.5333	1.7051	1.8439	1.9549
.7760	1.0855	1.3476	1.5667	1.7479	1.8960	2.0158
.7848	1.1014	1.3719	1.6002	1.7910	1.9487	2.0778
.7936	1.1173	1.3961	1.6338	1.8343	2.0019	2.1407
.8022	1.1330	1.4202	1.6773	1.8779	2.0557	2.2046
.8108	1.1486	1.4443	1.7009	1.9217	2.1100	2.2694
.8193	1.1641	1.4683	1.7345	1.9656	2.1647	2.3350
.8277	1.1795	1.4921	1.7680	2.0097	2.2199	2.4014
.8360	1.1947	1.5159	1.8015	2.0539	2.2754	2.4686
.8443	1.2099	1.5395	1.8350	2.0981	2.3312	2.5364
.8525	1.2249	1.5631	1.8683	2.1424	2.3872	2.6048
.8605	1.2399	1.5865	1.9016	2.1868	2.4436	2.6737
.8686	1.2547	1.6097	1.9348	2.2311	2.5001	2.7432
.8765	1.2694	1.6328	1.9678	2.2754	2.5567	2.8131
.8843	1.2839	1.6558	2.0007	2.3197	2.6135	2.8833
.8921	1.2984	1.6786	2.0335	2.3638	2.6702	2.9538
.8998	1.3127	1.7013	2.0662	2.4079	2.7270	3.0245

TABLE 3.—Continued

<i>s</i>	<i>K</i> = 2 Three classes	<i>K</i> = 3 Four classes	<i>K</i> = 4 Five classes	<i>K</i> = 5 Six classes	<i>K</i> = 6 Seven classes	<i>K</i> = 7 Eight classes	<i>K</i> = 8 Nine classes
.87	.9075	1.3269	1.7238	2.0986	2.4518	2.7838	3.0
.88	.9150	1.3409	1.7461	2.1309	2.4955	2.8405	3.1
.89	.9225	1.3549	1.7683	2.1629	2.5391	2.8970	3.2
.90	.9299	1.3687	1.7903	2.1948	2.5824	2.9534	3.3
.91	.9372	1.3824	1.8121	2.2264	2.6255	3.0096	3.3
.92	.9445	1.3960	1.8337	2.2578	2.6684	3.0655	3.4
.93	.9517	1.4094	1.8552	2.2890	2.7110	3.1212	3.5
.94	.9588	1.4227	1.8765	2.3200	2.7533	3.1765	3.5
.95	.9658	1.4359	1.8975	2.3506	2.7953	3.2315	3.6
.96	.9728	1.4490	1.9184	2.3811	2.8369	3.2861	3.7
.97	.9797	1.4619	1.9391	2.4112	2.8783	3.3402	3.7
.98	.9865	1.4747	1.9596	2.4411	2.9192	3.3940	3.8
.99	.9933	1.4874	1.9799	2.4707	2.9598	3.4472	3.9
1.00	1.0000	1.5000	2.0000	2.5000	3.0000	3.5000	4.0

$$^1 \text{The value tabled is } Z_K(s) = \frac{\sum_{t=1}^K ts^t}{\sum_{t=0}^K s^t} . \text{ The estimate of } s \text{ is the solution of the equation } Z_K(s) = \bar{x} , \text{ which}$$

found by entering the table in the appropriate column and reading on the left-hand scale that *s* which corresponds to the calculated $\bar{x}_K$.

for a segment of two adjacent age groups, this solution is

$$s = \frac{\bar{x}_1}{1 - \bar{x}_1} = \frac{N_1}{N_0}$$

and for *K* = 2, or in the case of three consecutive age groups in a segment, the solution is

$$s = \frac{-(1 - \bar{x}_2) + \sqrt{1 + 6\bar{x}_2 - 3\bar{x}_2^2}}{2(2 - \bar{x}_2)}$$

For 2 ≤ *K* ≤ 8, Table 3 may be used to find the estimate of *s*. For the data of the following example:

Coded age	Number in catch
0	118
1	73
2	36
3	14
Total number	241

$$\bar{X} = \frac{73 + 2(36) + 3(14)}{241} = \frac{187}{241} = .77593 .$$

Entering Table 3 with *K* = 3 and using linear interpolation

$$s = .5247, \text{ or rounded to three decimals} \\ = .525 .$$

If more accuracy is needed, or for samples with *K* > 8, the estimate could be found by an iterative process.

The variance of the estimate obtained for a segment consisting of *K* + 1 consecutive age groups is given by the formula

$$\text{Variance of estimate} = \frac{1}{n} \left[\frac{1}{s(1-s)^2} - \frac{(K+1)^2 s^{K-1}}{(1-s^{K+1})^2} \right]$$

so in the present case with *K* = 3 the estimate of variance is

$$\frac{1}{241} \left[\frac{1}{.525(1-.525)^2} - \frac{16(.525)^2}{[1-(.525)^4]^2} \right] = \\ \frac{1}{.525(1-.525)^2} - \frac{16(.525)^2}{[1-(.525)^4]^2} \\ \frac{1}{241} / [8.4422 - 5.1649] = .0012$$

The precision of estimation from a segment of the catch curve is substantially less than the precision obtained from using the entire catch curve; the above variance estimate is more than twice as large as the variance estimate of .000566 obtained using the complete catch curve. In fact, when the true survival rate in the population is .50 for all age groups then the efficiency of using just the first three age groups relative to using all age groups to estimate survival rate is only 43 percent. As mentioned earlier, however, circumstances may arise where it is necessary to estimate survival rate separately for different segments of the catch curve.

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Factors Related to Commercial Production of the Walleye in Red Lakes, Minnesota^{1,2}

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ABSTRACT

Growth of the walleye (*Stizostedion vitreum vitreum*) in Red Lakes, Minnesota, over a 17-year period was slower than in other waters of the Great Lakes region and fluctuated annually from 30.7 percent above to 42.2 percent below mean growth. Individual year classes varied considerably in growth rate. Age distribution in 3½-inch stretch-measure commercial nets varied extremely in 9 years' collections and was related to year-class strength and fishing intensity during periods when classes were available for catch. Abundance of different classes varied 23-fold. Annulus formation and resumption of growth occurred from mid-June to late July. Effective growing season did not exceed 4 months and for some individuals in some years was 2 months or less. The catch contained age-groups II–XII but consisted principally of groups IV–VIII. Seasonal changes in age distribution were dependent on growth rate and fishing effort. Total catch was strongly influenced by growth and seasonal distribution of fishing effort. Maximum availability to commercial nets was at a total length of 15.1 inches, but a large percentage of the catch was smaller fish. Total annual mortality rate after fish attained 15.1 inches total length was 0.66, but continued recruitment through group VIII caused apparent change in mortality rate with increasing age up to IX. Maximum harvest could be attained by concentrating fishing effort in the latter part of the growing season. Abundance indices derived from commercial catch will be strongly influenced by the seasonal pattern of fishing.

INTRODUCTION

A commercial fishery producing up to 1½ million pounds of fish annually is conducted in the Red Lakes of northwestern Minnesota. Of the seven species taken, the walleye (*Stizostedion vitreum vitreum*) provides the greatest poundage and revenue to the fisherman. All fish are caught by Indian residents of the Red Lakes Indian Reservation, within which the lower lake and two-thirds of the upper lake lie. Fish are taken with 3½-inch stretch-measure gill nets and marketed through a cooperative fishery plant. Smith and Krefting (1954) described the general nature of the operation and the production of the fishery over a 25-year period. Their work showed that the wide fluctuation in annual production of walleyes was dependent on strength of individual year classes and that the amount of fishing effort did not appear to influence population size or production in subsequent

years. Smith, Krefting, and Butler (1957) demonstrated through marking and recovery studies that walleyes in both the upper and lower lakes belong to the same population. Smith and Pycha (1960) studied the development of Red Lakes walleye during the early years of life. The early life history of the alewife (*Alosa pseudoharengus*) and the yellow perch (*Perca flavescens*) was studied by Pycha and Smith (1955), and the goldfish (*Hiodon alosoides*) fishery has been described by Grosslein and Smith (1959). The early history of the fishery and preliminary observations of some of the commercial species have been discussed by Van Oosten and Larson (1957).

The Red Lakes have a total area of 275,000 acres and consist of two oval basins connected by a narrow channel (Figure 1). They have a maximum depth of 35 feet and an average depth of approximately 18 feet. Shorelines are sandy and slope gradually into deep water. The lakes are moderately fertile, have a total alkalinity of 120 to 135 p.p.m., and are hot thermally. Water temperatures follow air temperatures closely during the summer, and strong currents are created by wind action.

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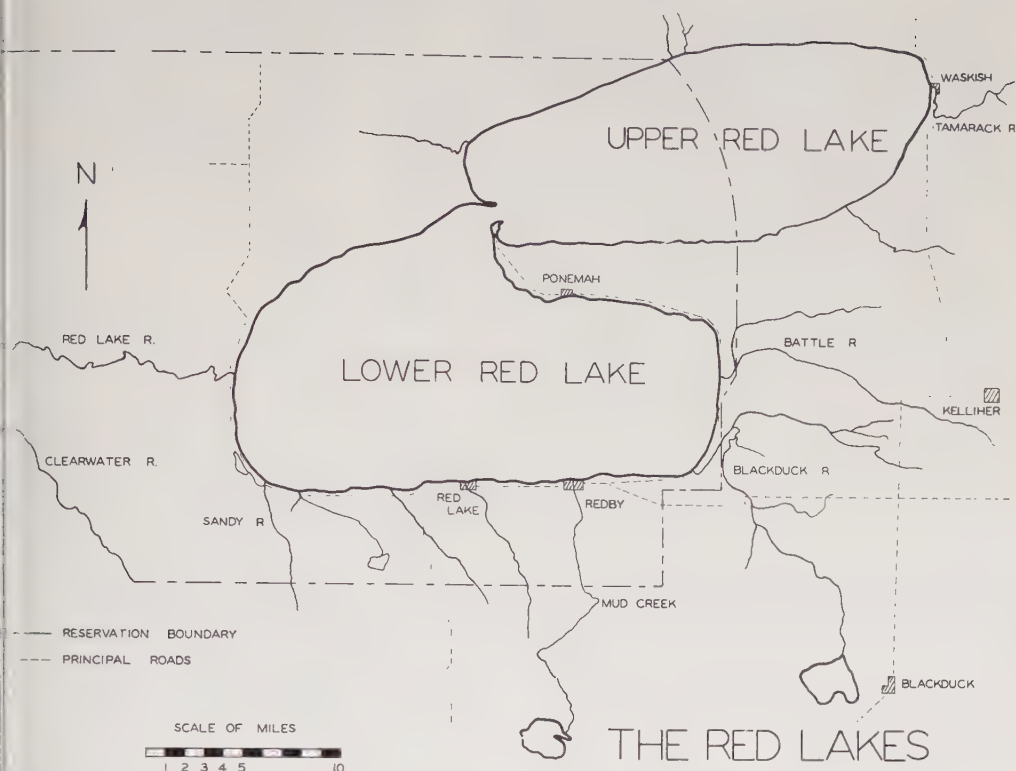


FIGURE 1.—Map of the Red Lakes, Minnesota.

the areas of submersed weeds are present in the shallow waters, especially on the south and west shores.

The importance of the walleye to the fishery has caused its fluctuations to govern the economic success of the fishing enterprise. For this reason it has been the subject of an intensive investigation over an 11-year period by the senior author. The present study is concerned with a description of the growth characteristics of the walleye, structure of the fishable population, and the factors which influence the contribution of various year classes to the annual walleye production. Since annual production has been shown to be heavily dependent on a few year classes, the problem of prediction of future harvest has been extended and means of obtaining maximum yields from each group have been considered. The authors are indebted to a number of field and laboratory assistants for their help in collecting and compiling the data presented herein. Robert Butler contributed to the early phases of the work, and Marvin Grosslein, John Lux, Robert Knapp, John Magnuson, and Bert Kramer gave substantial aid during

the latter period of the study. The U. S. Bureau of Indian Affairs and the management and fishermen of the Red Lakes Fishery Association have cooperated throughout the study, and financial aid has been given by the Ann Arbor Biological Laboratory of the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

MATERIALS AND METHODS

Collection of samples

Samples of fish from which scales and measurements for growth and age-distribution studies were taken have been collected from spawning runs, commercial production as it entered the fishery plant, and from experimental gill-netting. Spawning runs were sampled in 9 years at traps in the Black Duck and Tamarack Rivers and Mud Creek during spawn-taking operations. These samples were separated into males and females and included a total of 35,950 fish. Samples of walleyes were taken in 9 years by experimental gill nets set approximately 1 mile off Redby. These nets consisted of 250-foot gangs of five

alternate meshes ranging in size from 1½- to 4-inch stretch measure. Standard 3½-inch commercial nets 250 feet long were also fished simultaneously. A total of 4,817 fish were secured by experimental fishing.

A third set of samples was taken from the commercial catch. Since the catch for the entire lake is marketed through one fishery, a random selection from this catch was assumed to be a random representation of fish taken by commercial fishermen. In different years the catch was sampled on 12 to 28 separate days during the period from June 15 to August 25. The number of fish sampled in different years ranged from 6,655 in 1950 to 22,273 in 1957, with a total during the period of 113,242 fish. All commercial catches are made in 3½-inch stretch-measure nets and are delivered to the fishery plant in trucks. On sampling days care was taken to select 100-pound boxes of fish representing catches of all general areas in the lake without reference to exact location of catch or name of fisherman.

Age assessment and growth calculation

Growth calculations and age assessments were made from scale impressions on cellulose acetate slides. All scales were read twice, and in difficult groups, three times without reference to previous diagnosis. The age of the fish was determined from the number of annuli present on the scales, or if scale examination indicated that a season's growth had been completed but a new annulus had not yet formed, the total number of annuli present plus one was used as the designation of age. General growth calculations were made from samples of spawning runs and experimental gill nets, because only on these fish was sex determined. Fish of the 1947 year class taken in commercial gill nets were used for special growth analyses. Calculations were made from measurement of projected scale images (x42) recorded on paper tabs and applied to a nomograph designed to incorporate the body-scale relationship in accordance with the method outlined by Carlander and Smith (1944). Age distributions were determined from all commercial samples, selected spawning runs, and experimentally gill-netted fish. The catch statistics used in the calculation of total numbers of fish and total contribution of various year classes to the catch were taken from Smith and Krefting (1954) and from production records of the Red Lakes Fishery Association.

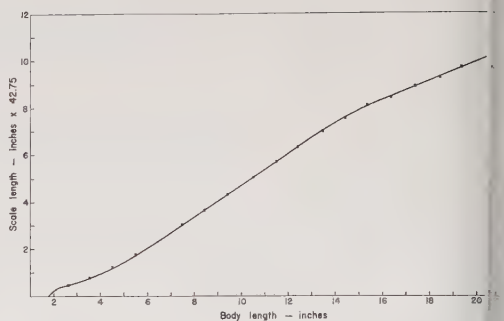


FIGURE 2.—Body-scale relationship of the walleye in Lower Red Lake.

The total length of all fish was measured to the closest 0.1 inch, and weight was recorded to the closest 0.1 ounce. Unless otherwise noted all lengths discussed in the following analyses are total lengths. Year class has been used to designate calendar year of spawning and age group to designate fish of particular ages without reference to year class.

DESCRIPTION OF GROWTH

Growth of Red Lakes walleyes was determined for 17 year classes collected in 9 calendar years. Of the 5,152 fish used for calculation of growth histories, 3,539 were taken from experimental gill-net samples and the remainder from spawning runs. Nine groups of fish were covered in the calculations, although some fish of greater age were observed. The old fish were omitted from the general summaries because their individual rates of growth varied greatly and the number was small. Fish from the commercial catch could not be used for growth calculations because the marketing procedure made it impractical to cut the fish to determine sex. Comparison of fish experimentally caught in commercial-type nets with those taken from the commercial catch indicated that fish of similar ages in the two catches had similar lengths at capture. Age distribution in experimental sets of commercial nets was comparable to distribution in the commercial catch. It was therefore assumed that the growth rate determined from spawning runs and experimental catches is representative of the growth of fish available to the commercial gear.

Body-scale relationship

Body-scale relationship was determined for 3,041 fish taken from the 1952 and 1955 commercial and experimental catches. Pre-

FIG. 1.—Body length—scale length ($\times 42$) ratio averaged for the fish in each 1-inch interval

[Total length in inches of fish is mean for the interval]			
Interval	Number of fish	Mean fish length	Mean scale length
2-2.9	64	2.60	0.46
3-3.9	230	3.52	0.77
4-4.9	200	4.51	1.24
5-5.9	116	5.46	1.77
6-6.9	124	6.42	2.34
7-7.9	163	7.46	3.01
8-8.9	104	8.42	3.67
9-9.9	114	9.43	4.30
10-10.9	88	10.50	5.04
11-11.9	186	11.48	5.72
12-12.9	228	12.40	6.34
13-13.9	332	13.47	6.99
14-14.9	342	14.41	7.56
15-15.9	156	15.32	8.11
16-16.9	244	16.32	8.47
17-17.9	150	17.39	8.90
18-18.9	82	18.42	9.30
19-19.9	52	19.35	9.70
20-20.9	44	20.37	10.37
21-21.9	16	21.46	10.59
22-22.9	6	22.03	10.75
Total	3,041	—	—

scanning of the data suggested that no mathematical function truly represented the average scale length at each body-length interval. To accommodate for changes in the relationship, fish in each 0.1-inch interval from 1.6 inches to 20.5 inches were aged. A three-point running average of the points was then plotted and a line through the points drawn by eye (Figure 2). Examination of the curve indicates that from a length of approximately 6 inches to 14 inches the relationship is essentially rectilinear, but with different slopes. Below 6 inches the relationship is curvilinear, and scale formation varies at an average length of 1.6 inches.³ Various functions calculated from the data do not represent the empirical relationships throughout the range. No attempt was made

to age fish less than 6 inches total length were taken from the lakes.

to use solutions of any particular function for calculation of length, but lengths at various annuli were determined empirically from the nomograph based on the curve developed in the manner described above. Back calculations by use of this method compared favorably with empirical lengths at time of annulus formation in younger fish. It is believed that this method of growth determination is superior for this population to calculations based on any assumed simple function.

The body length-scale length ratio of fish averaged for each 1-inch interval fell very close to the line projected on the basis of 0.1-inch groups (Table 1).

Average calculated length at each annulus

Upper and Lower Red Lakes.—Since small numbers of fish in the commercial catches come from Upper Red Lake, it was essential to know whether or not the fish from the two lakes grew at different rates. To make this determination, fish from the 1944, 1945, and 1946 year classes collected from the spawning runs in the Tamarack River in the upper lake and the Black Duck River in the lower lake in the spring of 1951 were compared (Table 2). Fish in age-groups V, VI, and VII were selected because any effect of precocious younger fish would thereby be minimized. There were differences presumably caused by sampling for the different groups from the two lakes. Since these differences were not consistent and showed no trend, it was concluded that fish taken in the two spawning runs were representatives of the same population. Tagging studies by Smith *et al.* (1952) confirmed the fact that fish in both lakes were part of the same population. The growth calculations set forth below, however, have been made exclusively on the basis of samples taken from the lower lake.

FIG. 2.—Calculated total length of walleyes at the end of each year of life of the 1944, 1945, and 1946 year classes taken from spawning runs in Upper and Lower Red Lakes in 1951—expressed in inches

Lake	Sex	Number of fish	Year of life						
			1	2	3	4	5	6	7
Lower	Male	73	5.3	8.1	10.0	12.2	14.0	15.3	16.0
Upper	Male	78	5.5	8.3	10.4	12.5	14.2	15.4	16.1
Lower	Female	98	5.4	7.4	10.0	12.3	14.6	16.4	17.5
Upper	Female	150	5.6	7.9	10.2	12.4	14.4	15.9	17.2
Lower	Male	66	5.4	8.0	10.7	12.9	14.4	15.2	—
Upper	Male	89	5.5	8.2	10.8	12.9	14.2	14.9	—
Lower	Female	31	5.2	8.0	10.9	13.4	15.0	16.3	—
Upper	Female	78	5.1	8.2	10.9	13.2	14.5	15.8	—
Lower	Male	224	5.6	9.1	11.6	13.1	13.9	—	—
Upper	Male	219	5.6	9.0	11.4	12.9	13.8	—	—
Lower	Female	12	5.5	9.1	11.6	13.1	14.8	—	—
Upper	Female	16	5.8	9.3	12.0	13.8	15.3	—	—

TABLE 3.—Grand average calculated total length of male walleyes in Lower Red Lake, 1940-1956 classes—expressed in inches

Year class	Number of fish	Year of life							
		1	2	3	4	5	6	7	8
1940	21	5.3	8.3	9.9	12.1	13.6	14.1	15.1	16.5
1941	20	5.2	7.4	10.3	12.4	13.3	14.3	15.7	16.8
1942	6	4.8	8.1	10.8	12.1	13.5	14.7	15.9	—
1943	21	5.0	8.3	9.9	11.9	13.7	15.1	—	—
1944	151	5.4	8.2	10.2	12.3	14.1	15.3	16.1	—
1945	177	5.4	8.1	10.7	12.9	14.2	14.7	15.5	16.2
1946	724	5.6	9.0	11.4	12.9	13.5	14.2	14.8	15.1
1947	500	5.7	8.9	11.0	12.0	13.2	14.0	14.4	14.7
1948	268	5.9	8.6	10.0	11.9	13.2	13.7	14.3	14.8
1949	371	5.8	7.8	10.3	12.0	12.9	13.7	14.3	15.0
1950	206	5.4	8.3	10.5	11.9	13.1	14.0	14.6	—
1951	268	5.6	8.2	9.9	11.7	13.1	14.0	—	—
1952	120	6.0	8.3	10.3	12.3	13.6	—	—	—
1953	78	5.6	8.6	11.0	12.7	—	—	—	—
1954	101	5.9	9.0	11.3	—	—	—	—	—
1955	45	6.1	8.8	—	—	—	—	—	—
1956	6	5.0 ¹	—	—	—	—	—	—	—
Total and grand average length	3,083	5.5	8.4	10.5	12.2	13.5	14.3	15.1	15.6

¹ Calculated from age-group I of the 1957 experimental gill-net catches (1956 year class); all other back calculations made on age-group II or older fish.

Grand average calculated length.—Grand average calculated lengths (Tables 3 and 4) of the walleyes in the 1940-1956 year classes were determined for the first nine seasons of growth. At age IX males and females had an average total length of 16.1 and 17.8 inches, respectively. The divergence in growth rate first appeared at the fifth annulus and became more apparent thereafter. When growth was described on the basis of the sum of mean average increment (Table 5, Figure 3), the divergence of growth between males and females began in the fourth year and was significant by the time the fifth annulus was at-

tained. By the time nine annual increments of growth had been added, the divergence between male and female was slightly less than 2 inches. The percentage annual increment varied from 50.5 percent in the females to 51.2 percent in the males during the second growing season to 6.8 percent in the females and 3.7 percent in the males during the ninth growing season. The rate of increase in males dropped off sharply during the sixth season and continued to decline, while in females it progressed steadily through the ninth season.

TABLE 4.—Grand average calculated total length of female walleyes in Lower Red Lake, 1940-1956 classes—expressed in inches

Year class	Number of fish	Year of life							
		1	2	3	4	5	6	7	8
1940	20	5.8	8.6	10.2	12.4	14.1	15.0	16.4	18.0
1941	20	5.4	7.5	10.2	12.3	13.4	14.8	16.7	18.4
1942	5	4.4	7.7	10.3	11.7	13.1	14.9	16.9	—
1943	22	5.4	8.5	10.2	12.3	14.6	17.1	—	—
1944	254	5.5	7.7	10.1	12.4	14.5	16.1	17.0	18.1
1945	37	5.2	8.0	10.5	12.4	13.7	14.3	15.3	16.4
1946	239	5.6	8.9	11.4	12.9	13.7	14.9	15.8	16.3
1947	224	5.6	8.9	10.9	12.0	13.5	14.7	15.1	15.6
1948	154	5.9	8.7	10.1	11.9	13.3	14.1	14.8	15.4
1949	222	5.7	7.8	10.2	12.0	13.0	13.9	14.9	15.8
1950	180	5.3	8.3	10.6	12.0	13.2	14.4	15.3	—
1951	211	5.5	8.1	9.9	11.6	13.1	14.4	—	—
1952	194	6.0	8.1	10.4	12.5	13.9	—	—	—
1953	95	5.7	8.8	11.2	13.0	—	—	—	—
1954	130	5.8	8.9	11.3	—	—	—	—	—
1955	47	6.0	8.7	—	—	—	—	—	—
1956	15	5.5 ¹	—	—	—	—	—	—	—
Total and grand average length	2,069	5.6	8.3	10.5	12.2	13.6	14.9	15.8	16.7

¹ See footnote 1, Table 3.

Fig. 5.—Grand average annual increment in length (inches) of male and female walleyes of age-groups I through IX in year classes 1940–1956

Male			Female		
Mean	Sum of means	Percentage increment	Mean	Sum of means	Percentage increment
5.50	5.50	—	5.52	5.52	—
2.82	8.32	51.27	2.79	8.31	50.54
2.18	10.50	26.20	2.20	10.51	26.47
1.76	12.26	16.76	1.78	12.29	16.94
1.28	13.54	10.44	1.45	13.74	11.80
0.86	14.40	6.35	1.28	15.02	9.32
0.80	15.20	5.56	1.12	16.14	7.46
0.72	15.92	4.74	1.00	17.14	6.20
0.60	16.52	3.77	1.18	18.32	6.88

Apparent change in rate of growth

In many studies on various species of fish it has been noted that fish taken in later years of collection appear to have grown more slowly during later years than fish taken during early years of life. In the present study this trend was present in Red Lakes walleyes but was not consistent in certain groups. Variations of annual growth rate in the various year classes checked to a considerable extent any tendency of this apparent change in rate of growth to build up in young year classes.

Examples of the 1947 year class were taken in successive years from both commercial and experimental nets. When fish taken from commercial gear were examined for growth in each year of collection, it was quite evident that precocious fish were caught early in life and that in later years of collection slower growing fish were taken (Table 6). Variations in calculated length at annulus II were as great as 0.8 inch between fish taken in the third year of life and those taken during the fifth season of growth. Calculated length at annulus III showed a difference as great as 1.0 inch between fish collected at 3 and 8 years of age. The change was progressive in the succeeding year of collection. It was also noted that slower growing fish were caught more frequently as each season progressed. Each year of collection except the last, the calculated length at each annulus was lower in fish taken in August collections than in June collections. Calculations made from August collections in one year were approximately the same or slightly higher than those from June collections in the following year. These data strongly suggest that the observed changes are caused by the taking of precocious fish in early years and a continued lag of the faster growing fish in each succeeding year in the commercial gear. The change within the season is ascribed to the

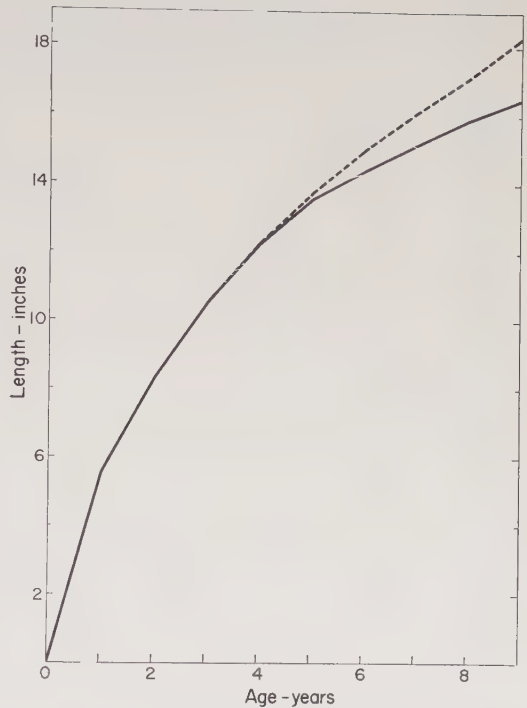


FIGURE 3.—Growth of male and female walleyes expressed as summation of grand average calculated increment in total length. Solid line, males; dashed line, females.

same mechanism. The fact that there is no downward trend between August collections and those of the following June is consistent with this assumption since there is no fishing during the intervening period. A shift in sex ratio, such as is described below, which reduces the relative number of faster growing females after annulus VI does not account for the decline in average growth rate because the trend is marked before this age. Fish of the 1947 year class taken in experimental nets from 1949 through 1955 show similar trends in the case of both males and females. The year classes of 1946, 1948, and 1949 taken in experimental nets also showed similar trends.

The data of Table 6 show a reversal of the downward trend in 1956 especially in calculated growth after annulus IV, and the trend within that season is also reversed. These changes are believed to be caused by a progressive decline in the efficiency of the gear which was noted in the 1956 season. The cotton webbing used in the fishery that year began to deteriorate as early as July 15 and was largely unfishable by the middle of August. The threads stretched easily so that larger fish

TABLE 6.—Average calculated length in inches of the 1947 year class of walleyes at each annulus successive months of collection and in different years of collection
[From unsexed fish taken in commercial gill nets]

Year and month of collection	Number of fish	Age group							
		I	II	III	IV	V	VI	VII	VIII
1949									
July	17	6.4	9.5	—	—	—	—	—	—
1950									
June	25	6.1	9.5	11.6	—	—	—	—	—
July	22	5.8	9.2	11.3	—	—	—	—	—
August	23	5.7	9.1	11.1	—	—	—	—	—
1951									
June	36	6.2	9.6	11.7	12.7	—	—	—	—
July	33	6.0	9.5	11.5	12.6	—	—	—	—
August	30	5.8	9.3	11.3	12.5	—	—	—	—
1952									
July	58	5.6	9.1	11.2	12.3	14.0	—	—	—
August	48	6.0	9.4	11.3	12.3	13.9	—	—	—
1953									
June	53	5.7	9.1	11.2	12.3	13.9	15.3	—	—
July	49	5.6	9.0	11.1	12.1	13.7	15.1	—	—
August	55	5.4	8.8	10.8	11.9	13.5	14.8	—	—
1954									
June	67	5.5	8.9	11.0	12.0	13.6	14.9	15.6	—
July	51	5.2	8.7	10.7	11.7	13.3	14.5	15.1	—
August	51	5.2	8.7	10.8	11.7	13.3	14.4	15.0	—
1955									
June	60	5.3	8.7	10.6	11.7	13.4	14.3	14.9	15.6
July	54	5.3	8.7	10.8	11.8	13.3	14.3	14.8	15.4
August	51	5.3	8.7	10.8	11.7	13.2	14.2	14.7	15.2
1956									
June	62	5.2	8.6	10.7	11.8	13.8	14.7	15.2	16.0
July	58	5.6	8.9	10.9	11.9	13.5	14.8	15.4	15.9
August	30	5.6	8.9	11.0	12.1	13.5	14.9	15.8	16.4

of the age group were more vulnerable to catch than smaller fish. As will be shown subsequently, the rate of catch also fell off instead of rising during the season as is characteristic in the Red Lakes. Since 1956 was a below-average year of growth, these effects were more apparent than would have been the case in a year of rapid growth.

From the observations reported here it appears that in an intensive gill-net fishery the time of sampling during the year and the age at which any year class is taken will influence the estimates of growth to a substantial degree. Unless each year class is sampled in a similar manner, comparisons between classes and averages of growth rate based on summa-

tion of growth in several classes will be so what in error.

Growth of individual year classes

Growth of individual year classes varied extremely (Tables 3 and 4, Figures 4 and 5). The total growth of fish in a year class at the third season of life appeared to be related to growth conditions during the second and third season. Variations seemed to be greater in the female than in the male. The significance of this difference in growth with relation to the fishery is considered and will be discussed in a later section. The slowest growing year class among those observed was the 1949 group, but it was clo-

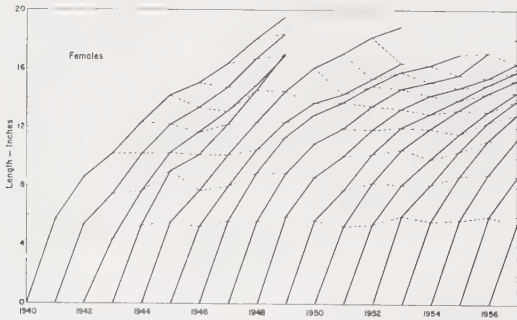


FIGURE 4.—Growth of females of the 1940-1956 year classes of walleyes in Red Lakes.

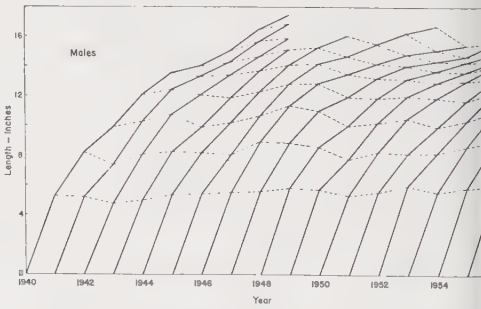


FIGURE 5.—Growth of males of the 1940-1956 year classes of walleyes in Red Lakes.

TABLE 7.—Percentage of fish of various ages taken in commercial 3½-inch nets with annuli formed at successive weekly intervals in 1951

[Number, males and females combined, in parentheses]

Week	Age group				
	III	IV	V	VI	VII
13-19	—	17 (6)	60 (5)	57 (7)	14 (14)
20-26	—	55 (20)	68 (25)	39 (18)	17 (12)
27-July 3	100 (2)	60 (5)	0 (3)	14 (7)	0 (2)
4-10	—	100 (3)	100 (6)	100 (5)	0 (2)
11-17	100 (11)	100 (11)	100 (3)	73 (11)	67 (12)
18-24	100 (2)	94 (17)	100 (22)	100 (9)	62 (13)
25-31	—	100 (1)	100 (4)	100 (4)	100 (4)
1-14	100 (15)	100 (16)	100 (15)	100 (15)	100 (17)

ewed by the 1951 class. At the end of the year of life fish of the 1949 group were smallest of the entire period (12.9 and inches for males and females, respectively). The fastest growing class, judged by length attained at the end of the fifth year, the 1944 year class. It had an average length of 14.5 inches for the females and 14.1 inches for males at the time of annulus formation. At 8 years of age the 1941 class was first in total length.

Time of annulus formation

Beckman (1943) indicated that the time of annulus formation in most species of fishes living in temperate lakes was early in the year after water temperatures had risen above 53° F. Since a similar assumption has generally been held in many cases where wall-eyes have been studied, fishes collected after the middle of June in short-term studies have been assigned on the basis that the annulus had already formed. Extreme variability in growth rate between individuals and discrepancies in strength-of-year-class estimates based on samples of different years suggest the possibility that late annulus formation might account for difficulty in reading and consequent irregularities in the data. It has been pointed out by workers using the scale method that late annulus formation in temperate climates shows a cessation of growth, which is usually associated with winter conditions, and subsequent resumption of growth in spring. Changes in growth rate associated with maturation of the sex organs and spawning activity often result in the formation of marks similar to characteristic winter marks and may be confused with them. Midsummer growth

TABLE 8.—Percentage of fish of various ages taken in commercial 3½-inch nets with annuli formed at successive weekly intervals in 1953

[Number, males and females combined, in parentheses]

Week	Age group					
	IV	V	VI	VII	VIII	IX and over
July 4-10	—	0 (2)	22 (18)	0 (7)	0 (1)	—
July 11-17	—	80 (5)	42 (45)	24 (29)	—	100 (2)
July 18-24	—	67 (12)	52 (64)	39 (41)	25 (4)	25 (4)
July 25-31	100 (1)	75 (8)	52 (42)	37 (19)	—	40 (5)
August 1-7	—	100 (12)	67 (36)	50 (26)	100 (1)	—
August 8-14	—	—	—	—	—	—
August 15-21	—	100 (10)	93 (46)	88 (16)	50 (2)	—

stoppage associated with extreme high temperature has also been reported.

In the Red Lakes samples of fish were taken throughout the fishing season in 1951 and 1953 to determine the time of annulus formation (Tables 7 and 8). These years were selected because the former was a year of good growth and the latter a year of poor growth. Time of annulus formation in individuals was related to the age of the fish, with younger fish forming annuli earlier than older fish. In 1951, a year of good growth, all group-III fish had formed annuli by the last week in June. Fish of the IV, V, and VI groups all showed annuli by the end of the first week in July. Age-group VII fish, however, had not all formed annuli until the last week of July. In 1953, a year of extremely poor growth, annuli had not been formed in any year class by the end of June. At the end of the first week in July, 22 percent of age-group VI had formed an annulus. By the end of the first week in August all of age-group V had formed annuli, but by the end of the third week in August fish older than age-group V had still not all formed annuli. Only half of group VIII and 33 percent of group VII had formed annuli by the end of the third week in August. The relatively small numbers of fish checked in the year of slow growth reduced the value of these conclusions somewhat, but they emphasize the extreme variability among individuals and age groups and the generally late formation of the annulus which occurred in this year.

The significance of late annulus formation is primarily related to errors in reading of scales, particularly in the years following a season of extremely poor growth and late annulus formation. In populations where very slow growth may be expected in some years,

TABLE 9.—*Annual growth of 801 walleyes in 1955 expressed as percentage of season's growth completed during successive weeks—July 11 to August 21*

[Fish taken in experimental nets]

Week	Sex	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
July 11-17	Male	—	32	28	24	10	—	8	27	—
	Female	—	—	12	18	37	25	14	11	—
July 18-24	Male	—	25	36	33	39	20	—	0	—
	Female	—	35	30	18	30	29	22	12	—
July 25-31	Male	—	41	34	37	56	25	0	0	—
	Female	—	49	41	59	28	28	80	9	12
August 8-14	Male	72	61	61	49	61	58	51	29	5
	Female	69	62	64	60	58	66	64	51	13
August 15-21	Male	70	65	66	63	71	63	31	40	5
	Female	77	81	63	67	69	75	78	45	—

the validity of age assessment cannot be assured unless several years' collections representing the same year classes are examined.

The causes for late annulus formation are presumably those which determine slow growth for the season as a whole. Limited and nonquantitative observations have suggested that years of late annulus formation are usually years in which early summer feeding has been poor. During these years it has been observed that fish are in poor condition and most of them have empty stomachs until mid-July or later. Years of good growth and early annulus formation are related to an early start of ample feeding. The time of annulus formation does not appear to be related directly to temperature since in the Red Lakes temperatures are well above the presumed threshold for the resumption of growth by mid-June or earlier. In many years when fish have not yet formed an annulus by the middle of July they have been subjected to temperatures higher than 65° F. for more than a month. The ecological and physiological significance of these observations has not been explored but would appear to be a fertile field of investigation.

Growth within the season

The percentage of a season's increment in growth in length which has been attained on any particular calendar date will be related to the time of annulus formation and to general conditions controlling growth rate. A year of good growth and one of poor growth will be examined in detail to define the range of growth rate within a season. Growth during the season was determined by weekly intervals during the 1955 and 1956 seasons (Tables 9 and 10). Percentages were calculated from total increment as shown in fish taken in the season following the respective year. In view of the apparent slower growth of fish taken in latter years of life already demonstrated, the percentages are based on a total increment that is too small and therefore the percentages are maximum. In a year of good growth (1955) there was no obvious trend in percentage of annual increment attained by any particular date which could be associated with age of the fish. During a season of poor growth (1956) fish of the older groups tended to complete a greater percentage of growth by August than the younger fish. In a year of moderate or poor growth a greater percentage

TABLE 10.—*Annual growth of 479 walleyes in 1956 expressed as percentage of season's growth completed during successive weeks—June 27 to August 21*

[Fish taken in experimental nets]

Week	Sex	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
June 27-July 3	Male	11	14	27	40	19	39	—	—	—
	Female	—	19	25	27	31	—	—	—	—
July 11-17	Male	43	12	9	42	34	—	43	39	—
	Female	20	—	—	—	42	—	46	—	—
July 18-24	Male	—	41	—	25	52	—	54	36	75
	Female	—	50	41	46	54	75	83	77	91
July 25-31	Male	47	43	61	51	60	66	38	43	31
	Female	48	50	46	59	57	38	63	107	—
August 1-7	Male	57	53	57	43	68	52	46	57	—
	Female	48	61	55	57	70	53	54	—	57
August 15-21	Male	64	75	87	69	78	90	91	120	—
	Female	66	76	70	80	123	107	74	59	—

TABLE 11.—Percentage deviation of increment in growth in various calendar years from mean increment of the period 1941–1956

	Male	Female	Average
1	+ 6.2	+ 7.0	+ 6.6
2	-24.5	-25.0	-24.8
3	+21.9	+22.7	+22.8
4	+18.6	+20.2	+19.4
5	-17.2	-22.1	-19.7
6	+ 5.6	+11.8	+ 8.7
7	+29.2	+32.2	+30.7
8	+25.9	+25.1	+25.5
9	+ 4.2	+ 0.5	+ 2.4
10	-42.8	-41.5	-42.2
11	+ 3.8	+ 2.9	+ 3.4
12	- 3.7	0.0	- 1.8
13	-30.1	-33.8	-31.9
14	- 3.0	- 6.0	- 4.5
15	+ 8.4	+ 6.5	+ 7.5
16	- 2.5	- 0.3	- 1.4

age of the annual increment was attained at the end of the first week in August than in years of good growth. In a year of poor growth up to 66 percent of the season's total increment was attained by August 1. In a year of good growth a smaller percentage had generally been attained by that date. Among fish which were partially or wholly available to the fishery (age-group V and older) 50 percent or more of the season's growth had been attained by August 1. A comparison of the sexes in different years did not show any marked difference between them. Females had a tendency to put on more of the season's growth early in the summer but individual rates varied greatly. Growth of different age classes during the same season varied considerably but was not consistently related to the general growth history of the class.

Variations of growth in different calendar years

Growth and total increment in all age groups of walleyes varied markedly from year to year and influenced the production of the fishery. During years of poor growth fish readily available to the commercial gear produced a smaller average contribution for the number of individuals taken than was the case in a year of good growth. A more important influence on production is that a smaller proportion of fish about to enter the commercial catch do so in years of poor growth because the fishing season is short and coincides with the season of growth. In age groups or sizes which must live an extra year before they are caught because slow growth keeps them from entering the fishery, natural mortality exacts a loss which may be out of proportion to the increased size of the remain-

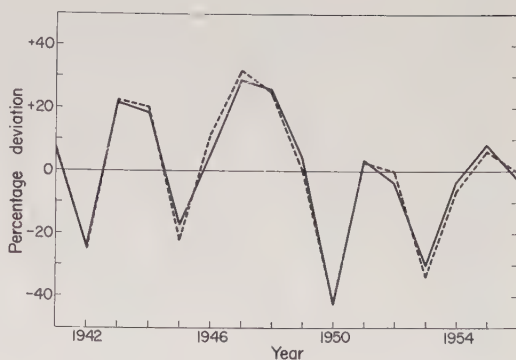


FIGURE 6.—Percentage deviation in separate calendar years from mean annual increment—1941–1956 period. Solid line, males; dashed line, females.

ing individuals. In order to determine the extent to which slow growth may influence availability of fish, investigation of variation in average growth rate in different calendar years has been made on the basis of percentage deviation from mean increment of all years considered in the manner outlined by Hile (1941). Increments during each calendar year of all age groups except age-group I were used in the compilation, since Smith and Pycha (1960) showed that increments during the first season of life are not closely correlated with those made by older fish.

Estimates of the percentage deviation from the mean annual increment of the period 1941–1956 were made for each sex (Table 11, Figure 6). During this period the minimum increment was 42.8 and 41.5 percent below the mean in 1950 for males and females, respectively. The year of maximum average increment was 1947, when males were 29.2 and females were 32.2 percent above the mean. There was good agreement between males and females in the different calendar years except that females tended to deviate somewhat more in years of much better or poorer than average growth. When the collections for separate years were calculated independently on the basis of combined sexes (Table 12) there was essentially good agreement on the trend in growth rate for the separate calendar years. Discrepancies are presumed to be due to sampling error. The apparent discrepancy for 1947 in the fish collected during 1953 is attributed to a small sample of fish representing growth in that year. The relatively close agreement between the estimate of growth rate in different calendar years made from the individual collections of succeeding cal-

TABLE 12.—Percentage deviation from mean annual increment in length of walleyes in various calendar years
[Each year of collection calculated separately and males and females averaged]

Calendar year	Year of collection						
	1950	1951	1952	1953	1954	1955	1956
1944	+12.3	—	—	—	—	—	—
1945	—18.3	—	—	—	—	—	—
1946	—9.6	—2.3	—3.3	—	—	—	—
1947	+21.4	+16.2	+15.8	—7.1	+16.1	+14.4	—
1948	+15.2	+18.4	+16.8	+14.2	+9.7	+14.6	+10.1
1949	—14.8	+1.8	—2.8	—2.7	—0.9	—6.5	—17.9
1950	—	—34.1	—37.9	—34.1	—31.4	—38.0	—45.6
1951	—	—	+11.5	+19.0	+19.5	+19.9	+20.5
1952	—	—	—	+10.7	+8.6	+11.3	+11.9
1953	—	—	—	—	—21.6	—17.6	—8.3
1954	—	—	—	—	—	+1.8	+6.7
1955	—	—	—	—	—	—	+23.0
1956	—	—	—	—	—	—	—

endar years is strong evidence of the consistency and accuracy of age assessment.

Different age groups responded differently to the factors influencing growth rates in different calendar years. In general the younger groups showed less response to adverse factors than the older groups although the trends were usually in the same direction. Fish of age-group IV and older showed a greater percentage decline in increment during poor years than those of age-groups II and III. Although the deviation from the mean annual increment of the period 1941–1956 fluctuates rather widely, there has been a downward trend through these years. Increment during 1943, 1944, 1946, 1947, and 1948 was greater than during any subsequent year. The lows of 1950 and 1953 were both below those of 1940 and 1945. This trend toward slower growth in each year is also reflected in the slower growth of year classes after 1945. Although the data of Van Oosten and Deason (1957) covering the growing seasons of 1933–1938 are not comprehensive enough to permit calculation of relative growth in different seasons during this period, there was substantially greater total growth of the individual year classes represented in their data than in those year classes treated in the present study. This difference suggests that during the 1930's average growth rates were higher than during the 1950's. Causes for this downward trend are not readily discernible but examination of broad weather trends shows that during the 1930's growing seasons on the average were longer and that total degree days were greater than in the late 1940's and 1950's. During the early 1950's populations of perch were much greater than in most previous seasons and abundance of goldeye, a suitable forage species, declined. While the relationship of these factors to the observed changes in growth

rate cannot be defined by available data, their direct influence estimated, trends during the course of the present study and comparison with work done previously on Red Lake indicate clearly that growth varies enough over a span of years to require periodic adjustment of procedures governing exploitation on the basis of new data. These adjustments would be most necessary in regulations relating to length at capture. Hile (1954) observed a similar long-range trend in growth of white eye in Saginaw Bay and noted that it was greater during the 1930's than before 1920.

Reliability of age determination

Determination of age from scales of Red Lakes walleye was accomplished by use of the usual criteria applied to ctenoid scales. In general, cutting over of circuli in the lateral fields was the best means of locating the annulus. In years of very poor growth, however, the annulus was not necessarily complete and in older fish confusion of other regularities with a true annulus increased the difficulty of reading. The validity of the signment of year marks was attested by close similarity of growth pattern of fish selected in different calendar years but assigned to the same year class. Since fish were selected over a 9-year period, it was possible to follow the individual year classes and check their relative abundance in succeeding samples. The variations in abundance between the different year classes were consistent in various collections, as will be shown in the subsequent section. Continuous collection throughout the growing season made it possible to establish the time of annulus formation and determine the exact age of fish which formed the annulus late or which showed little growth. As pointed out above, the goodness or poorness of growth in different calendar years

TABLE 13.—Weight of walleyes at successive 1-inch intervals calculated from the length-weight curve

Length (inches)	Weight (pounds)	Increment (pounds)	Percentage increment
6	0.07	0.03	74.4
7	0.11	0.04	60.0
8	0.16	0.05	50.3
9	0.23	0.07	43.2
10	0.31	0.09	37.9
11	0.42	0.11	33.7
12	0.55	0.13	30.4
13	0.70	0.15	27.7
14	0.87	0.18	25.4
15	1.08	0.20	23.4
16	1.31	0.23	21.8
17	1.58	0.27	20.3
18	1.88	0.30	19.0
19	2.21	0.34	17.9
20	2.59	0.38	16.9
21	3.00	0.42	16.0
22	3.46	0.46	15.2
23	3.96	0.50	14.5
24	4.51	0.55	13.9
25	5.11	0.60	13.3

calculated from collections of succeeding years, showed that the method of age assignment was reliable.

A further criterion was the occurrence of a narrow area of growth increment on the scale laid down in the 1950 season. This characteristic was so distinctive on the majority of fish collected during the several ensuing seasons that it formed a landmark by which assignment of annuli could be checked for accuracy.

Length-weight relationship

The length-weight relationship of walleyes was determined from 1,604 fish measured to the closest 0.1 inch and weighed to the closest ounce. Data were available from fish 6.4 inches to 22.0 inches in total length measured from the tip of the tail lobes to the tip of the snout. The length-weight relationship is described by the formula

$$W = 0.0002786 L^{3.04957}$$

where W = weight in pounds and L = length in inches. Weights of fish at 1-inch intervals calculated from this relationship are shown in Table 13. Extrapolation of this curve below 6.4 inches does not give the accurate weights which have been determined from age-of-the-year fish taken in various seasons (Smith and Pycha, 1960). From a length of 14 inches to a length of 22.0 inches empirical averages of fish grouped by 1-inch intervals compared favorably with the calculated length up to 17.5 inches. Beyond this the empirical weights are less than would be predicted. The small size of the samples of fish above 18.0 inches accounts in part for the discrepancy.

TABLE 14.—Growth in weight (pounds) of male and female walleyes in the Red Lakes—expressed as calculated weight at time of annulus formation

[Weight derived from summed grand average calculated increments in length]

Age group	Male			Female		
	Length	Weight	Percentage increment	Length	Weight	Percentage increment
I	5.50	0.05	—	5.55	0.05	—
II	8.32	0.18	256.0	8.31	0.18	242.3
III	10.50	0.36	103.4	10.51	0.36	103.9
IV	12.26	0.58	60.5	12.29	0.59	62.5
V	13.54	0.79	35.5	13.74	0.82	39.5
VI	14.50	0.95	20.7	15.02	1.08	31.2
VII	15.20	1.12	17.9	16.14	1.34	24.4
VIII	15.92	1.29	15.2	17.14	1.62	20.2
IX	16.52	1.44	11.9	18.32	1.98	22.6

It will be noted from Table 13 that between 13 and 17 inches the rate of increase in weight decreases from 27.7 to 20.3 percent. Since this is the length range of maximum availability to the commercial nets, increases in weight will have considerable significance in appraising the effect of any increased size limit on production.

Condition factor or ponderal index has been widely used to appraise changes in body shape of fish or changes in weight at different seasons or between different waters. Variations in stomach contents, state of the gonads, changes associated with length, and other factors have for the most part made calculation of condition factor undesirable except for special studies where the sources of variation could be controlled or measured. Changes in condition throughout the fishing season in the Red Lakes walleye population were determined in various years from June 15 through August. There was a trend toward a higher index of condition as the season advanced, but the pattern of change varied extremely in different years. Average weight of spawning fish of a specified length was somewhat greater than it was for fish taken during the commercial fishing season.

Growth in weight

Growth in weight of walleyes of both sexes (Table 14, Figure 7) was approximately the same during the first 4 years of life, but thereafter the rate of increase declined in the males. It also decreased in females but more slowly. The percentage increase in weight was from 256 and 242 percent during the second season of growth to 11.9 and 22.6 percent in the ninth season for males and females, respectively. At the time of ninth annulus formation males had an average weight of 1.44 pounds and females a weight of 1.98 pounds.

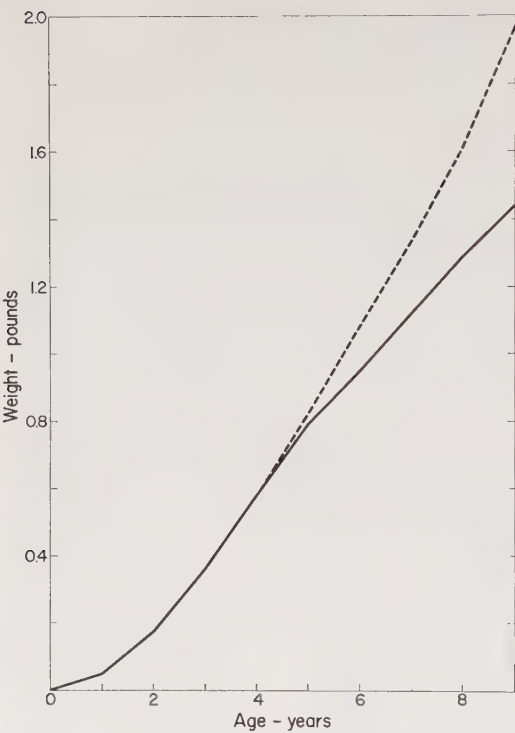


FIGURE 7.—Weight of male (solid line) and female (dashed line) walleyes at time of annulus formation in succeeding age groups—based on calculated weights and lengths.

Growth in weight of various year classes varies with differences in their respective length increments. Difference in males at fifth annulus in different classes may be as great as

0.23 pound and in females 0.28 pound. In the ninth annulus the difference may be 0.10 pound for males and 0.98 pound for female.

Comparison with growth in other waters

The growth of walleye pike has been compared with growth in other large waters of the north-central region of the continent (Table 15). Growth during the 1940–1956 period in Red Lakes was slower than in other waters reported by various authors. It is also slower than that reported by Van Oosten and Deason (1957) for Red Lakes during the 1933–1938 period (apparent slower growth during the first year is due in part to direct proportion method of calculation). When data from Red Lakes are compared to those from Lake of the Woods, it is apparent that through age group VI growth was slower during the 1940–1956 period in Red Lakes but roughly comparable during the 1933–1938 period. Since the earlier period in Red Lakes covers a series of years comparable to that reported for Lake of the Woods, it is possible that long-range fluctuation in the latter lake may show a cline similar to that in Red Lakes. In any case it cannot be assumed on the basis of available data that Red Lakes walleyes grow more slowly than those in Lake of the Woods. Growth reported for Lac la Ronge in Saskatchewan is comparable to early Red Lakes records but faster than growth demonstrated during the present study.

In Lake Erie, Saginaw Bay, and Green Bay growth is much faster than in Red Lakes. This advantage is marked by the end of the

TABLE 15.—Calculated total length at succeeding annuli of walleyes from various waters—expressed in inches.

Water	Sex	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
Red Lakes	Male	5.5	8.4	10.5	12.2	13.5	14.3	15.1	15.6	16.1
	Female	5.6	8.3	10.5	12.2	13.6	14.9	15.8	16.7	17.8
Red Lakes ¹ (Van Oosten and Deason, 1957)	Male	4.4	8.5	11.4	13.5	14.8	15.9	—	—	—
	Female	4.4	8.6	11.6	13.7	15.2	16.7	—	—	—
Lake of the Woods ¹ (Carlander, 1945)	Male and female	6.4	9.3	11.5	13.5	14.9	16.7	18.2	19.9	21.6
Lake Erie ¹ (Deason, 1933)	Male and female	6.0	9.7	12.1	15.1	18.0	—	—	—	—
Green Bay ²	Male	7.3	11.4	14.2	16.2	17.9	19.2	20.2	20.8	21.5
	Female	6.7	10.8	14.2	16.5	18.5	20.2	21.7	23.0	24.2
Saginaw Bay (Hile, 1954, 1930– 1940 group)	Male	6.4	12.0	15.8	18.1	19.5	20.6	21.4	21.9	22.7
	Female	6.4	12.0	16.3	18.9	21.3	22.9	24.3	25.4	26.3
Lac la Ronge (Rawson, 1957)	Male and female	—	9.2	11.1	12.9	14.9	16.7	18.4	20.0	21.5

¹ Adjusted from original data to total length in inches.
² Unpublished data compiled by the junior author from fish taken 1949–1957.

Table 16.—Sex ratio of walleyes taken from experimental gill nets in Red Lakes, 1955–1957

Age group	Number of males	Number of females	Number of males per 100 females
	87	118	74
	95	123	77
	137	145	94
	141	123	115
	142	172	83
	138	167	83
	87	79	110
	81	54	150
	36	18	200
	13	4	325
Total	957	1,003	95

and growing season in both Saginaw Bay and Green Bay. Fish in Saginaw Bay are on average 10 percent larger at this time than those in Red Lakes, and by the end of the eighth growing season males have a 40 percent and females a 51 percent greater size. Causes of this difference in growth rate may be related to length of growing season or to available space factors, since the populations in both Saginaw and Green Bays are subject to colder and less fertile water than Red Lakes. Heavy cropping of Red Lakes fish, which includes a high percentage of precocious fish, especially females, reduces the apparent growth of older fish. It has been suggested that continued heavy cropping of precocious fish in Red Lakes may have a selective effect that results in a long-range reduction in growth rate, but available data do not provide evidence of this genetic change.

SEX RATIO

The sex ratio of 1,960 fish of age-groups I–IX taken in experimental gill nets during June, July, and August of 1955, 1956, and 1957 was determined. Fish older than age-group IX were extremely scarce (Table 16), and there was much variation between age groups and years of collection. When all age groups for all years were combined the ratio was 95 males to 100 females. During the first 6 years of life there was a preponderance of females. Age-group IV, in which females predominated, is an exception, but the high calculated abundance of males was based entirely by the 1955 sample. From age-group V through age IX there is an increasing preponderance of males until in the ninth and tenth age groups there are 325 males per 100 females.

In the spawning runs which occurred in the streams tributary to the Red Lakes, males predominated strongly. During some years they were observed to exceed females by 10 to 1 or

more. The run of 1949 in the Black Duck River, which was completely checked, had a ratio of 184 males to 100 females. The run of Mud Creek, also completely checked in 1951, had a ratio of 368 males per 100 females. Random samples of other runs made over a 9-year period are not reliable since there is a tendency for the different sexes to be more strongly represented at different periods of the run, but in all cases there was a strong predominance of males.

This predominance of males in stream runs, which has been observed in most other Minnesota runs and which is at variance with the conditions of the Red Lakes population as a whole, is probably the result of several factors. Few females are mature until after the sixth season of growth, whereas the large majority of males are mature after the fifth season. There is also a substantial number of precocious males of age-groups III and IV in the runs. A second important factor is the earlier harvest of females by the fishery. Females are almost completely available to the fishery at some time during their sixth season of growth, while males are not fully available until their seventh season or later. The effect of this differential is demonstrated by the predominance of females through age-group VI and the rapid increase in the proportion of males in the older age groups represented in the catch of experimental nets.

There is some evidence that the females have a greater natural longevity than the males since the few very large and old fish taken are predominantly females.

The conditions in Red Lakes differ from those reported by Carlander (1945) for Lake of the Woods and by Hile (1954) for Saginaw Bay. In both cases a relative increase in the proportion of females with advance in age was noted as early as age-group VI. Hile found that in age-groups VIII–XV only 16.1 percent of all fish were males. These authors attributed the trend to a greater mortality rate among the males.

SIZE AND AGE AT MATURITY

Determination of average age at maturity from fish caught in June, July, and August was difficult because the state of the gonads of fish which will spawn for the first time the following spring often cannot be evaluated with certainty. All estimates of size and age at maturity have therefore been made from spawning runs in streams. This method has serious limitations because precocious young

TABLE 17.—Length-frequency distribution of male and female walleyes in the spawning runs in streams entering Red Lakes—1949–1958

Size class (inches)	Male		Female	
	Number	Percentage	Number	Percentage
11.2–11.5	5	<0.1	—	—
11.6–11.9	21	<0.1	—	—
12.0–12.3	165	0.6	—	—
12.4–12.7	503	1.8	2	<0.1
12.8–13.1	1,153	4.2	3	<0.1
13.2–13.5	2,338	8.6	12	0.1
13.6–13.9	3,116	11.6	25	0.3
14.0–14.3	4,150	15.4	116	1.3
14.4–14.7	4,063	15.1	285	3.1
14.8–15.1	3,358	12.5	547	6.0
15.2–15.5	2,720	10.1	833	9.2
15.6–15.9	1,595	5.9	956	10.5
16.0–16.3	1,112	4.1	1,034	11.4
16.4–16.7	755	2.8	958	10.6
16.8–17.1	541	2.0	760	8.4
17.2–17.5	419	1.6	601	6.6
17.6–17.9	281	1.0	478	5.3
18.0–18.3	250	0.9	378	4.1
18.4–18.7	141	0.5	349	3.8
18.8–19.1	103	0.4	350	3.9
19.2–19.5	56	0.2	333	3.7
19.6–19.9	22	<0.1	262	2.9
20.0–20.3	17	<0.1	248	2.7
20.4–20.7	4	<0.1	155	1.7
20.8–21.1	3	<0.1	108	1.2
21.2–21.5	1	<0.1	70	0.7
21.6–21.9	1	<0.1	49	0.5
22.0–22.3	—	—	36	0.4
22.4–22.7	—	—	21	0.2
22.8–23.1	—	—	22	0.2
23.2–23.5	1	<0.1	15	0.2
23.6–23.9	—	—	10	0.1
24.0–24.3	—	—	9	<0.1
24.4–24.7	—	—	7	<0.1
24.8–25.1	—	—	18	0.2
25.2–25.5	—	—	7	<0.1
25.6–25.9	—	—	3	<0.1
26.0+	—	—	6	<0.1
Total	26,894	—	9,066	—

fish enter the run and there is a wide range in strength of year class. The previously mentioned difficulty in securing a random sample from the runs further limits accuracy.

Of 35,960 fish checked during the spawning runs in Tamarack River, Black Duck River, and Mud Creek in the 10-year period 1949–1958, 26,894 were males and 9,066 females (Table 17). Males as small as 11.2 inches were mature and entered the runs in most seasons, but were present in small numbers. During the entire period 15.2 percent of the mature males checked were less than 13.6 inches in length and approximately 65 percent were between 13.6 and 15.5 inches in length. Estimation of age from length measurements on the basis of grand average calculated lengths suggests that a substantial number of age-groups III and IV were in the runs and that a large proportion of all males had completed six seasons of growth or less.

The females were not as closely grouped and were substantially larger than the males. The smallest mature female taken was 12.5 inches long and the largest 26.0 inches. Ten

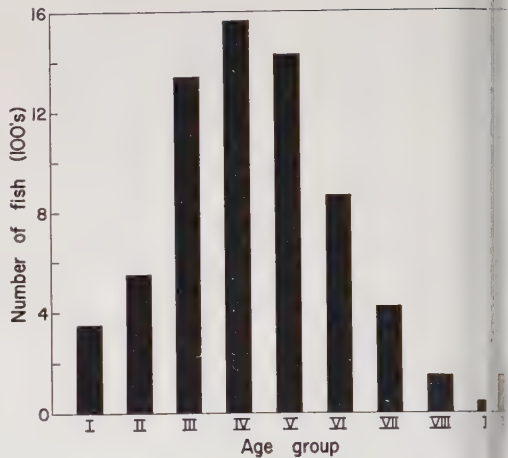


FIGURE 8.—Sum of number of fish per 30 experimental nets each year (1949–1956).

and seven tenths percent of females were 12 inches or less in total length and 56.8 percent between 15.2 and 17.2 inches. Approximately 89 percent of the females in the run had completed six or more seasons of growth, and more than 65 percent had completed seven or more.

Selected groups of fish in which age was determined from scales in general support the estimates made above. It would appear that most of the males are mature by the end of the sixth season and most of the females by the end of the seventh season, but that does a small proportion of females spawn up after the sixth season is completed. The wide range in growth rates and strength of year classes makes generalizations concerning maturity difficult and of limited applicability to many problems.

AGE DISTRIBUTION

Experimental catches

The age-group distribution of the walleyes in Red Lakes was estimated from experimental and commercial catches. All experimental catches were made in the standard experimental nets, but fishes younger than age-group IV were apparently not caught in proportion to their abundance in the population (Table 18, Figure 8). Although the 1-inch meshes in the smallest gill net took during their second season of growth, the graded meshes took proportionately less of age-groups I, II, and III than were present in the population. This selection, how-

18.—Number and percentage of fish caught per unit of 30 experimental nets each year summed for period 1949–1957

[Percentages in parentheses]

Year									Total
1949	1950	1951	1952	1953	1954	1955	1956	1957	
4 (0.5)	26 (3.3)	18 (2.2)	28 (4.4)	46 (5.3)	11 (1.0)	137 (18.1)	56 (14.1)	19 (3.6)	345
102 (12.4)	32 (4.0)	37 (4.6)	50 (7.9)	52 (5.9)	101 (9.3)	30 (3.9)	88 (22.3)	60 (11.3)	552
404 (49.1)	253 (31.5)	101 (12.5)	74 (11.7)	85 (9.7)	103 (9.4)	94 (12.4)	46 (11.7)	182 (34.1)	1,342
88 (10.7)	388 (48.2)	398 (49.5)	88 (13.9)	215 (24.6)	163 (14.9)	97 (12.8)	56 (14.1)	73 (13.7)	1,566
124 (15.1)	64 (7.9)	239 (29.6)	266 (41.9)	150 (17.1)	321 (29.3)	134 (17.5)	52 (13.3)	77 (14.4)	1,427
64 (7.8)	34 (4.2)	11 (1.4)	120 (18.9)	235 (26.8)	165 (15.1)	150 (19.8)	39 (9.8)	52 (9.8)	870
20 (2.4)	6 (0.7)	1 (0.2)	8 (1.3)	87 (10.0)	182 (16.6)	61 (7.9)	39 (9.8)	22 (4.1)	426
12 (1.4)	2 (0.2)	—	—	3 (0.3)	43 (3.9)	43 (5.6)	10 (2.4)	36 (6.8)	149
0.5 (0.5)	—	—	—	3 (0.3)	2 (0.2)	15 (1.9)	9 (2.2)	12 (2.3)	45
822	805	805	634	876	1,091	761	395	533	6,722

nearly constant, and strong or weak year classes could be followed from year to year. In order to equilibrate estimates of age-distribution in different years, the catch has been reported in terms of take of 30 experimental net sets made in July and August of the various years (Table 18). In two of the years group-IV fish were taken in great numbers, and the largest percentage was represented by age-group IV in 1951 when it comprised 49.5 percent of the entire experimental catch. In 1949 age-group III made 20.1 percent and in 1952 age-group V, 41.9 percent of the total. After the fifth year of the percentage of fish in the older age groups fell off rapidly. The largest numbers of age-group VI were taken in 1953 when the group formed 26.8 percent of the catch. Age-group VII the greatest representation in 1954 when 16.6 percent were of that group. Fish of age-group IX and older combined in all years less than 2.3 percent of the catch. The range of numbers in the various age groups in successive years varied 16-fold in age-groups IV and V, and over 10-fold in age-group VII. After the fifth year of life the contribution of any particular age class to the population varied extremely. Although these estimates are subject to substantial sampling error, the trends exhibited year classes are consistent with other information.

Commercial catches

The age composition of the commercial catch in 1949–1957 was determined from 14,407 measured fish and 9,407 fish for which age was determined, or a total of

108,951. After the age of fish from the scale samples had been ascertained, they were grouped in 0.4-inch intervals and the percentage of each group in each interval was applied to the total number of fish measured in this interval to determine the age distribution of the entire sample. The average weight of the fish in each age group was applied to the number of fish in the group in the entire sample to determine the proportion by weight of each age group. The total weight of the sample was then compared to the total weight of the catch and the appropriate factor applied to permit estimation of the total number of fish in each group in the entire commercial catch. By this procedure it was possible to get the total weight and the total number of individuals in each age group in the catch. Since cull fish⁴ were sampled separately from the "regulars" and separate weights determined for them, they were treated separately by the same procedure and then added to the totals. The data were grouped by months because it was noted, as will be demonstrated below, that the age composition of the catch varied in the different months. During each month samples were taken at 2- to 5-day intervals to permit assessment of changes in age distribution within the season and to compensate for heavy runs of particular age groups and sizes on particular nights. Observation of variation in runs indicated that a short sampling period in any year would be ineffective for estimation.

In order to make better comparisons be-

⁴ Culls are fish less than approximately 12.5 inches, which are graded and weighed separately.

TABLE 19.—Total production of walleyes and number of summer net-lifts (5-net units) in Red Lakes—1940–1957

Year	Lifts	Walleye (pounds)	Year	Lifts	Walleye (pounds)
1940	6,614	799,753	1949	9,905	660,124
1941	8,086	929,528	1950	12,768	383,447
1942	12,934	940,887	1951	12,449	556,229
1943	14,816	823,827	1952	7,856	654,210
1944	8,454	969,587	1953	6,883	537,500
1945	10,596	872,694	1954	7,918	634,611
1946	11,092	911,464	1955	9,373	644,454
1947	12,393	977,428	1956	10,835	636,444
1948	10,083	928,512	1957	8,723	666,391

two years and to correct for differences in total fishing effort, the age distribution was recorded in terms of total number of individuals of each age group caught per 100 net-lifts.⁵ Total production and total number of lifts were taken from fishery records (Table 19). On the basis of these values, the average annual catch of each age group was estimated (Table 20).

The commercial catch was primarily dependent on fish in groups V and VI except in some seasons when groups VII and VIII contributed heavily. The extreme variation in contribution of each age group in different years was a function of both the strength and the growth history of different year classes. Slow-growing classes contributed more heavily as age-group VI than as age-group V, while faster growing classes contributed more as age-group V. Age-group V contributed from 12.1 percent (1953) to 64.0 percent in 1951;

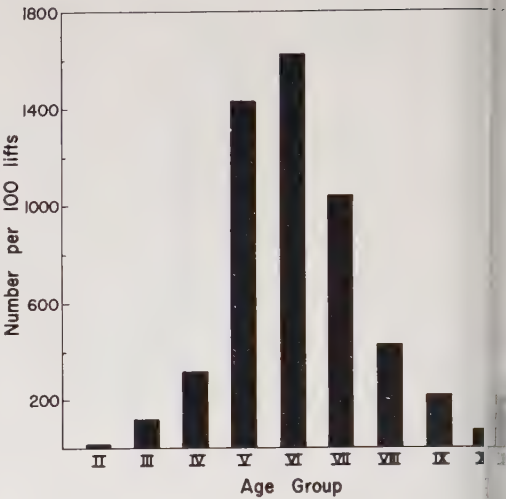


FIGURE 9.—Average number of walleyes in various age groups per 100 5-net lifts per year of commercial fishing in the Red Lakes—1949–1957

age-group VI contributed 6.8 percent (1949) to 52.6 percent (1953); and age-group V contributed from 1.8 percent (1949) to 43.3 percent (1954). Age-group VIII contributed 29.7 percent to the 1955 catch, or approximately twice as much as in the next highest year (1954). On the basis of the 9-year average catch per 100 lifts (Table 21, Figure 9), age-group VI were most prominent (52.6 percent), followed by age-group V (26.4 percent) and age-group VII (19.2 percent). The other age groups combined made up 24.7 percent of the catch.

⁵ A lift is five 300-foot nets fished for 1 night.

TABLE 20.—Number and percentage of each age group of walleyes per 100 net-lifts of commercial 3½-inch gear—Red Lakes, 1949–1957

[Percentages in parentheses]

Age group	Year of capture							
	1949	1950	1951	1952	1953	1954	1955	1956
II	63 (1.2)	1 (-)	1 (-)	5 (0.1)	-	5 (0.1)	28 (0.5)	9 (0.2)
III	348 (6.8)	92 (3.9)	24 (0.6)	70 (0.9)	49 (0.7)	58 (0.8)	99 (1.8)	27 (0.6)
IV	342 (8.7)	680 (29.1)	690 (17.5)	289 (3.9)	250 (3.5)	170 (2.3)	195 (3.5)	141 (6.3)
V	1,807 (35.2)	326 (13.9)	2,521 (64.0)	3,371 (46.0)	861 (12.1)	1,068 (14.7)	628 (11.4)	683 (15.9)
VI	1,642 (32.0)	518 (22.1)	269 (6.8)	3,055 (41.7)	3,726 (52.6)	1,559 (21.4)	1,359 (24.6)	1,073 (25.0)
VII	93 (1.8)	472 (20.2)	173 (4.4)	191 (2.6)	1,992 (28.1)	3,152 (43.3)	1,113 (20.1)	1,123 (26.2)
VIII	396 (7.7)	70 (3.0)	167 (4.2)	150 (2.0)	83 (1.2)	1,131 (15.5)	1,641 (29.7)	519 (12.1)
IX	392 (7.7)	84 (3.6)	39 (1.0)	173 (2.4)	122 (1.7)	87 (1.2)	403 (7.3)	483 (11.2)
>IX	46 (0.9)	98 (4.2)	53 (1.4)	31 (0.4)	6 (0.1)	51 (0.7)	64 (1.1)	108 (2.5)
Total	5,100	2,340	3,936	7,335	7,089	7,281	5,530	4,166
Five-net lifts	9,905	12,768	12,449	7,856	6,883	7,918	9,373	10,835

¹ Less than 0.5 fish.

21.—Number of walleyes caught per 100 5-net of commercial 3½-inch gill nets in the Red Lakes—summation for years 1949–1957

Age group	Total number (sum)	Average per year	Percentage
	127	14	0.3
	1,054	117	2.2
	3,308	368	6.8
	12,928	1,436	26.4
	14,565	1,618	29.8
	9,374	1,042	19.2
	4,834	537	9.9
	2,005	223	4.1
	671	75	1.4
	48,866	5,430	—

Age in age distribution during season

The age distribution in the commercial fishery varied as the season progressed from May through September in each year. In general there was a shift from older age groups to younger groups as growth brought the latter more completely into the range of the commercial nets (Table 22). The extent of this

shift was conditioned by growth during individual seasons, strength of year classes, and to a certain extent by the relative intensity of the fishing load. In all years of the period except 1954, the take of age-group IV increased in relative numbers as the season advanced. This change was as great as from 17.2 to 40.1 percent in 1950, but in other years it was less marked. In 1954, when fishing was carried over into September, the take of age-group IV increased through August and then declined. This change may have been caused by the method of calculation rather than actual conditions. In some years, especially toward the latter part of the period, this trend was also noticeable in the V group. During 1949, when a high proportion of the V group was available to the nets throughout the season, the catch of these fish fell off as the summer progressed. In early years of the sampling period VI-group fish became less numerous in the catch as the season progressed. During

22.—Percentage contribution of various age groups of walleyes to the commercial catch in succeeding months of the 1949–1957 fishing seasons in the Red Lakes

Month	Age group								
	II	III	IV	V	VI	VII	VIII	IX	>IX
May	1.0	4.9	5.6	37.6	32.4	2.0	7.2	8.5	0.8
	1.2	6.3	7.0	33.7	33.4	1.8	8.7	6.8	1.1
	2.2	19.5	10.7	30.3	23.1	1.1	5.8	7.3	—
June	—	1.7	17.2	9.8	27.7	21.6	9.8	5.4	6.8
	0.1	1.7	26.9	15.8	23.4	24.2	1.4	2.8	3.8
	—	8.2	40.1	14.3	16.8	14.1	0.3	3.4	2.8
July	—	0.1	8.3	51.9	12.4	8.3	9.7	6.0	3.2
	—	0.6	15.8	62.6	8.4	5.1	5.5	0.4	1.5
	—	0.8	21.1	68.0	4.2	2.9	1.8	0.4	0.8
August	—	0.8	3.0	42.6	42.7	2.8	3.8	3.5	0.8
	0.1	1.0	4.1	42.9	43.8	3.1	1.9	2.6	0.5
	0.1	1.0	4.2	53.4	37.2	1.6	1.3	1.2	—
September	—	—	1.2	10.3	47.7	34.6	1.9	4.1	0.1
	—	0.2	1.9	10.6	55.1	28.2	2.0	1.8	0.2
	—	1.3	5.5	13.9	53.1	25.3	0.3	0.7	—
October	0.1	0.6	0.7	4.7	26.1	46.4	18.7	1.6	1.1
	0.1	1.3	2.6	9.7	16.1	49.7	18.8	1.1	0.7
	0.1	0.8	2.7	18.5	22.6	39.9	13.6	1.2	0.6
November	—	0.3	2.1	17.3	23.3	41.2	14.0	1.1	0.7
	0.3	1.0	2.2	10.1	21.0	22.6	34.5	7.3	1.0
	0.7	2.4	3.9	9.7	20.5	22.0	29.7	9.9	1.2
December	0.5	1.9	4.1	12.8	27.9	18.0	28.0	5.6	1.2
	0.2	0.9	2.7	12.7	28.7	18.6	29.1	5.8	1.2
January	—	0.2	3.4	7.9	28.5	29.6	14.4	13.6	2.5
	0.2	0.5	4.1	16.0	25.0	27.5	11.8	12.2	2.7
	0.4	1.1	11.7	22.2	22.1	21.6	10.6	8.0	2.3
February	—	2.6	5.8	23.0	24.8	16.5	15.8	6.2	5.4
	0.1	3.0	6.4	22.8	24.7	19.8	14.6	4.4	4.0
	0.6	7.8	13.9	35.0	19.0	15.6	4.9	1.6	1.6

TABLE 23.—Average monthly percentage composition of the commercial catch of walleyes in the Red Lakes, 1949–1957

Age group	Month			
	June	July	August	September
II	0.2	0.3	0.5	1.2
III	1.0	1.7	3.2	6.9
IV	5.2	7.9	12.3	5.2
V	20.0	25.3	30.2	20.1
VI	28.9	27.7	26.3	25.0
VII	22.8	20.2	15.6	20.3
VIII	13.6	10.3	7.7	16.3
IX	6.0	4.9	3.2	4.7
>IX	2.6	1.7	1.2	1.0

the latter part of the period this trend was less marked and in 1953 and 1955 was reversed. Fish 7 years old and older became noticeably less abundant toward the close of the fishing season in all years. In seasons when the most abundant year classes in the fishery had histories of rapid growth, these shifts were most noticeable, especially in age-groups IV and V. Among year classes in which growth was slow throughout life, recruitment continued over a 3-year period and tended to mask the shift.

When the data for all years are combined (Table 23), age-groups III, IV, and V show a progressively increased representation as the season progressed, while group VI showed a slight decline and the VIII and older groups declined sharply. The September estimates are not strictly consistent with the trend noted above because fishing in this month was done in only 3 years of the 9-year period and variations in year-class strength affected the average more than in other months.

Contribution of individual year classes to the fishery

On the basis of the calculations made above it has been possible to estimate the total contribution of various year classes to the fishery between their second and ninth year in both total numbers and total weight (Tables 24 and 25). The maximum yield from any year class observed through its entire period in the fishery was that of the 1947 class which contributed 1,100,000 individuals and 1,228,000 pounds. The minimum contribution was made by the 1945 year class which, exclusive of groups II and III, produced only slightly more than 136,500 individuals and 156,000 pounds. The strongest year classes (1946, 1947) contributed heavily in numbers from the fifth through the seventh year. The 1946 year class made the maximum contribution in any single year when 345,000 pounds of V–annulus fish were produced. The 1947 group, while not

contributing as heavily in any single year, continued to produce heavily through the eighth year and as age-group IX made the largest contribution of any year class at that age. In year classes up to and including 1949 the greatest contributions were made by age-groups V or VI. Thereafter, age-groups VI and VII gave maximum yields. It is apparent that a year class may produce its greatest yield at different ages, depending both on its rate of growth and strength of the class. Since the fishery is run on a quota basis the simultaneous presence of two or more strong year classes in the fishery causes their contribution to be stretched out over a greater period. If a single strong year class is in the fishery, the greatest production will occur earlier and then taper off rather rapidly due to the intensification of the fishing pressure which is exerted to fill the quota.

Only a small proportion of the total numbers and weights of fish in any year class is produced at ages II and III. The importance of weak year classes in any year's production is evident from a comparison of the contributions of weight by age-groups V and VI. The 1945 class, which was a small contributor, failed to support the fishery during the 1946 and 1951 seasons as other year classes did in the following years. Since it had been preceded by a relatively poor class, the 1950 total production was near an all-time low (Table 24). From the foregoing data it is evident that sustained commercial production is dependent on a succession of good year classes, and that the general level of abundance will be strongly influenced by the strength of individual classes.

Estimation of year-class strength

The estimates of the strength of the 1945–1956 year classes were expressed as the percentage of the average number of fish per 100 fish per season of age-groups IV through IX for each year class (Table 26). The average of the estimated sums for all classes was used as a base, and the percentage of this base which each year class represented formed an index of its relative strength. Since all year classes were not represented by complete data for age groups from IV through IX, various comparisons were made to estimate the strength. Data for the 1945–1948 year classes are complete. The catch per hundred units of gross IV fish from the 1944 year class was based on the regression from age-groups IV to V from the 1945 year class. This procedure

TABLE 24.—Number of walleyes produced from each year class at different ages—classes 1940-1955

[Expressed as thousands]

Age group								Total
II	III	IV	V	VI	VII	VIII	IX	
—	—	—	—	—	—	—	38.9	—
—	—	—	—	—	—	39.2	10.7	—
—	—	—	—	—	9.2	8.9	4.8	—
—	—	—	—	162.7	60.3	20.7	13.6	—
—	—	—	179.1	66.2	21.6	11.8	8.4	—
—	—	33.9	41.6	33.5	15.0	5.7	6.9	136.6
—	34.5	86.9	313.8	240.0	137.1	89.5	40.7	942.5
6.2	11.7	85.9	264.8	256.5	249.6	168.2	57.2	1,100.1
0.1	3.0	22.7	59.2	123.5	113.5	62.7	19.4	404.1
—	5.5	17.2	84.6	141.5	134.9	59.0	—	442.7
0.4	3.4	13.4	65.0	129.8	92.9	—	—	—
—	4.6	19.4	87.5	119.0	—	—	—	—
0.4	9.5	22.3	145.0	—	—	—	—	—
2.7	3.4	48.1	—	—	—	—	—	—
1.1	25.0	—	—	—	—	—	—	—
1.4	—	—	—	—	—	—	—	—

less than 100 fish.

There was employed because the growth histories of these year classes were similar. The catch for the 1943 year class was estimated by comparison with the sums of groups VI-IX in the 1944 year class. Sums for the 1940-1942 year classes were estimated by comparison with comparable data from the 1946 year class. Growth histories of these year classes were more comparable to that of the 1946 year class than to the 1947 year class. The 1940 and 1941 estimates were added by application of the ratios of the total fishing effort withstood by these year classes to the total effort applied to the 1946 year class. These two classes passed through the fishery during a period of much higher fishing intensity than did the 1946 year class. The catch of group-VIII and IX fish from these classes was probably much lower than it would have been had fishing intensity been as low as it was in the 1946 year class passed through the

fishery. The 1949-1952 year-class sums were estimated by comparison of summations of the catch per 100 lifts of group-IV and older fish to comparable figures from the 1947 year class. Growth histories of these year classes were more similar to the 1947 than to the 1946 year class. Strengths of the 1953-1956 year classes were estimated from the catches per 30 experimental net units by the same procedure as was used for the 1949-1952 year classes. The estimates are most reliable for the 1945-1948 year classes and are less accurate for classes further removed from this period.

Of the 17 classes observed during the present study, that of 1947 was the strongest, but it was closely followed by the 1940 class. The weakest class was that of 1942 which was followed by the 1945 group. Variation in strength between the greatest extremes was 23-fold. There appeared to be little relation-

TABLE 25.—Poundage of walleyes produced from each year class at different ages—classes 1940-1955

[Expressed as thousands of pounds]

Age group								Total
II	III	IV	V	VI	VII	VIII	IX	
—	—	—	—	—	—	—	72.7	—
—	—	—	—	—	—	68.7	21.2	—
—	—	—	—	—	12.0	4.7	3.7	—
—	—	—	—	229.4	99.0	38.3	23.5	—
—	—	—	211.4	93.4	37.2	17.7	14.9	—
—	—	—	—	43.2	20.0	7.6	9.5	156.4
—	—	31.2	44.9	292.6	165.6	111.5	55.7	1,075.0
—	22.1	82.2	345.3	278.4	286.1	210.0	98.9	1,227.9
2.1	6.2	72.1	274.1	130.3	134.0	93.7	33.5	467.3
—	1.5	17.8	56.5	152.3	184.7	92.0	—	519.7
—	2.7	11.7	76.3	162.8	134.6	—	—	—
0.1	1.9	11.1	61.8	147.0	—	—	—	—
—	2.4	14.1	98.4	—	—	—	—	—
0.1	4.9	33.8	149.2	—	—	—	—	—
1.0	2.4	44.7	—	—	—	—	—	—
0.4	15.8	—	—	—	—	—	—	—
0.5	—	—	—	—	—	—	—	—

less than 100 pounds.

TABLE 26.—Estimated strength of 1940–1956 year classes—expressed as percentage of average strength of all classes

Year class	Number ¹	Percentage of average
1940	11,869	211
1941	3,666	65
1942	560	10
1943	8,182	145
1944	4,666	83
1945	1,298	23
1946	9,782	174
1947	13,063	232
1948	4,563	81
1949	5,112	79
1950	3,506	62
1951	3,761	67
1952	5,803	103
1953	3,126	56
1954	9,801	174
1955	4,579	81
1956	2,397	43
Average	5,631	—

¹ Estimated sum of annual average catch per 100 5-net sets of age-groups IV through IX in each class.

ship between the strength of a year class and the strength of the one immediately following it. Weak classes often preceded strong classes, but the 1947 class, the strongest of the period, was preceded by a strong class.

SELECTIVITY OF NETS

The catch characteristics of commercial 3½-inch nets are an important consideration in Red Lakes because walleyes, yellow perch, and other species must be taken simultaneously. Ideally, a minimum size limit on fish should be set to permit the maximum yield in weight consistent with market needs and the use of efficient gear. Gill nets are sometimes assumed to have rather sharp selection at the lower length limits and to permit minimum size regulation of fish by fixing the mesh size of the net. For spiny-rayed fishes such as the

TABLE 27.—Percentage of total catch of walleyes from commercial gear in each 0.4-inch interval and sum of the average annual number per 100 5-net lifts in 1949–1957

Length (inches)	Number	Percent-age	Length (inches)	Number	Percent-age
8.0–9.1	13	0.02	15.6–15.9	4,703	9.46
9.2–9.5	16	0.03	16.0–16.3	3,571	7.18
9.6–9.9	40	0.08	16.4–16.7	2,210	4.44
10.0–10.3	40	0.08	16.8–17.1	1,500	3.02
10.4–10.7	100	0.20	17.2–17.5	957	1.92
10.8–11.1	131	0.26	17.6–17.9	594	1.19
11.2–11.5	273	0.52	18.0–18.3	442	0.89
11.6–11.9	362	0.73	18.4–18.7	307	0.62
12.0–12.3	538	1.08	18.8–19.1	241	0.48
12.4–12.7	645	1.29	19.2–19.5	102	0.21
12.8–13.1	880	1.77	19.6–19.9	126	0.25
13.2–13.5	1,483	2.98	20.0–20.3	88	0.18
13.6–13.9	3,073	6.18	20.4–20.7	57	0.11
14.0–14.3	5,568	11.20	20.8–21.1	36	0.07
14.4–14.7	7,275	14.63	21.2–21.5	14	0.03
14.8–15.1	7,763	15.61	21.6–21.9	10	0.02
15.2–15.5	6,561	13.19	22.0–23.9	9	0.02

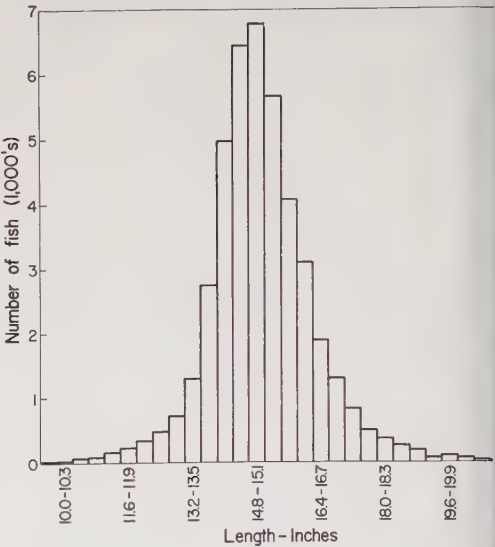


FIGURE 10.—Number of walleyes in each 0.4-inch interval per average 100 5-net lifts of commercial gear—summed for years 1949–1956.

walleye, this lower limit is not well defined. Many fish are tangled in the net or caught by hard body parts at sizes below those which might be expected to be retained in mesh of a particular dimension. The length-frequency distribution of 113,242 walleyes caught in commercial nets was plotted and expressed as numbers per hundred net lifts in each 0.4-inch interval (Table 27, Figure 10). Both limbs of a catch curve representing fish from 8.0 to 23.9 inches are similar. The left limb rises somewhat more abruptly than the right limb, indicating no sharp selectivity. Fish were numerous in the 14.8- to 15.1-inch size interval, and a plot by 0.1-inch intervals of this group shows the point of maximum vulnerability to be 15.1 inches total length. It is presumed that an alteration in mesh would displace the curve to the right or left without alter its general shape appreciably. When the catch of the nets is viewed on the basis of weight, the peak of the catch curve is at 1.2 pounds.

It is apparent from a comparison of length distributions of the commercial catch and the spawning runs that fish become less vulnerable after they exceed a particular size since large fish are relatively more plentiful in the spawning run than in the size groups of commercial runs which are presumed to be mature. The effect of this decrease in vulnerability to the 3½-inch nets has not been de-

TABLE 28.—Percentage of each age group and percentage of all walleyes caught in the Red Lakes in commercial (3½-inch) nets below 15.1 inches total length in June, July, and August, 1949–1957

Age group	Year								
	1949	1950	1951	1952	1953	1954	1955	1956	1957
<u>June</u>									
II	—	—	—	—	—	100	100	100	—
III	—	100	100	100	—	100	100	100	—
IV	—	90.9	89.5	100	100	100	100	84.3	—
V	—	69.2	74.6	87.4	84.9	87.5	88.9	93.2	—
VI	—	25.0	64.8	57.7	48.0	53.6	67.2	53.4	—
VII	—	12.1	9.0	27.4	28.5	37.3	54.2	45.4	—
VIII	—	0.0	13.1	51.3	18.0	16.8	33.4	24.2	—
IX	—	0.0	0.0	27.1	16.9	0.0	18.8	20.6	—
and >X	—	0.0	0.0	0.0	—	0.0	0.0	0.0	—
Total catch	—	33.6	56.3	69.3	43.8	40.0	51.7	45.3	—
<u>July</u>									
II	100	100	—	100	—	100	100	100	—
III	100	100	100	100	100	100	100	100	—
IV	100	94.8	98.8	100	100	100	100	92.2	—
V	57.7	70.2	81.0	84.6	93.9	100	93.6	79.6	—
VI	27.6	29.8	70.1	50.6	58.3	77.8	74.7	58.4	—
VII	19.0	7.4	24.7	28.6	35.7	51.7	47.0	40.0	—
VIII	4.7	0.0	10.9	29.5	9.8	33.3	41.6	30.9	—
IX	1.9	0.0	0.0	21.1	0.0	27.4	27.1	16.5	—
and >X	0.0	0.0	0.0	0.0	0.0	—	22.7	14.9	—
Total catch	43.0	47.2	74.7	65.6	54.4	58.4	57.1	48.9	—
<u>August</u>									
II	100	—	100	100	—	100	100	100	100
III	100	100	100	100	100	100	100	100	100
IV	89.4	95.6	94.2	94.7	100	100	96.0	92.1	79.4
V	45.5	68.1	76.6	66.2	83.3	92.9	89.2	69.8	57.8
VI	27.7	33.1	48.5	46.3	57.6	75.4	69.7	46.6	54.1
VII	27.6	22.8	16.6	14.5	36.5	53.1	50.2	38.5	29.8
VIII	0.0	0.0	0.0	40.2	0.0	34.7	43.4	35.6	16.5
IX	0.0	0.0	0.0	22.6	0.0	45.9	20.5	16.9	0.0
and >X	0.0	0.0	0.0	—	—	0.0	20.6	22.6	0.0
Total catch	38.8	65.1	75.3	58.8	58.1	64.2	59.9	52.1	—

ed, but it may result in a higher proportion of very large females in the population than would otherwise occur (Smith *et al.*, 1952).

A large percentage of fish in the commercial catch is below the size of full availability to the nets during the entire fishing season (Table 28). In the various years (1950–1956) 33.6 to 69.3 percent were less than 15.1 inches during June. In July, 43.0 to 74.7 percent and in August, 38.8 to 75.7 percent were below the size of full availability.

In no year were any of the fish in age-groups II and III taken at the size of complete availability. In some years none of the age-group IV fish taken were 15.1 inches or above at the time during the season. Not until fishing in age-group VIII were they completely available in any season, and in some seasons the fish of age-groups IX and X were not at the size of complete availability. This slow rate of year classes since 1947 to attain size of maximum vulnerability is explained by the low rate of growth rates of fish during the season.

As the season progressed no clear-cut trend

appeared in the catch of fish below the size of maximum availability. In years of very poor growth the percentage of fish in the older groups below 15.1 inches tended to increase as the season progressed. In years of good growth this trend was less pronounced and was even reversed. The intensity of the fishing in August, the relative strength of year class, and total abundance of fish interacted to produce the variations noted. When fishing intensity is high and fish of fully available size are not abundant, the percentage of small fish is higher.

SEASONAL TRENDS IN CATCH RATE

In 6 of the 9 years sampled the catch per unit of effort of walleyes in terms of number of fish taken (Table 29) was greater at the end of the season than during the first month of fishing. This trend was brought about primarily by the increase in size of individuals during the season which brings a higher percentage of small fish within range of catchability by the nets, and was most pronounced in years when large numbers of young fish were of a size immediately below full avail-

TABLE 29.—Number of walleyes caught in the Red Lakes per 100 5-net lifts in June, July, August, and September—1949–1957

Year	Month				Season average
	June	July	August	September	
1949	—	7,021	4,512	2,865	5,100
1950	3,909	2,057	2,124	—	2,341
1951	1,993	4,104	4,828	—	3,936
1952	3,484	8,780	11,922	—	7,335
1953	5,304	6,608	8,711	—	7,089
1954	5,352	5,590	8,434	9,498	7,281
1955	5,130	4,938	5,770	7,205	5,530
1956	5,626	4,933	2,820	—	4,166
1957	5,350	6,320	6,155	—	6,059

ability to the gear. The catches of 1949, 1950, and 1956 did not show this trend although the catch rate was higher in August than in July 1950. In 1949 very few fish were available in the younger groups, especially representatives of the 1945 year class which were entering as fish of age-group IV in August. The extremely poor growing season of 1950 (Table 11) probably accounts for the failure of the catch rate to increase markedly during that season, and the decrease in net efficiency during July and August of 1956, which has been described previously, presumably reduced the normally expected catch in those months. In 1957 growth began unusually early. Of fish taken in experimental gill nets in June, all but one fish of age-groups I to V showed some marginal growth on the scales. By mid-July all fish of age-groups I to IV showed growth increments of 0.5 inch or greater, and all fish of age-group V at least 0.3 inch. The early onset of growth undoubtedly accounts for much of the increase in catch rate from June to July of that year. The slight decline in August cannot be explained on the basis of available data.

The heaviest catches for individual sets are made during the hottest periods of the summer, presumably because change in water temperature and location of food cause maximum fish movement. During these periods more large fish in proportion to the total are taken. Since these catches are sporadic and not consistent, no attempt has been made to analyze them individually and assign definite causes of greater catch.

Causes of changes in catch per unit of effort during the fishing season

If the observed changes in catch per unit of effort from month to month during the fishing season were due entirely to or even principally to changes (increases) in the rate of movement of the fish, a catch curve of an in-

TABLE 30.—Number of 1947 year-class walleyes 100 5-net lifts during each month of fishing, 1957

Age group	Year of capture	Month				Season average
		June	July	August	September	
II	1949	—	73	56	63	—
III	1950	65	36	175	—	—
IV	1951	166	650	1,018	—	6
V	1952	1,483	4,546	6,365	—	3,7
VI	1953	2,528	3,639	4,625	—	3,7
VII	1954	2,481	2,778	3,363	4,549	3,1
VIII	1955	1,767	1,463	1,615	2,613	1,7
IX	1956	766	601	249	—	—
X and >X	1957	287	280	97	—	2

dividual year class during the fishing season could show a negative mortality rate. In order to simplify consideration of this problem the 1947 year class alone was followed through its history in the fishery (Table 30).

In 1949 the catch per 100 net units of age-group II was so small that it appeared the catch was entirely accidentals. From 1950 through 1955, the catch per 100 units was higher in the last month of the fishing season than in the first, apparently indicating a negative mortality rate; but in 1956, the apparent mortality rate was again positive. The percentage of each age group caught at a size below full vulnerability to the gear indicates that at all ages from II through IX a sizeable proportion of the 1947 year class was below full vulnerability to the gear (Table 28). It is therefore possible that since the period of fishing covers approximately the period during which growth occurs, the apparent change in availability is a result of increased vulnerability due to growth during the season rather than any marked change in movements of the fish.

In order to check this possibility growth of the commercial fish of the 1947 year class was back-calculated. The number of fish 1.1 inches or greater in length at annulus VI per 100 units of effort was then calculated for June, July, and August of each year from 1953 through 1956 (Table 31, Figure 1). The same calculation for fish 15.1 inches or greater at annulus VII was made for 1953 through 1956 (Table 32, Figure 11). By considering fish greater than 15.1 inches, or fish fully vulnerable to the gear are used, thus eliminating the effect of recruitment on apparent mortality rate. As was expected, except for June and July 1953 the catch per 100 units was lower in each successive month during the fishing season. The average total mortality rate of fully available fish appears to be ab-

FIGURE 31.—Decline in the catch of 1947 year-class walleyes larger than 15.1 inches at annulus VI from 1953 through 1956

Month and year	Age group	Fish greater than 15.1 inches		Total number of fish caught	Catch per 100 lifts	Number of lifts	Annual survival (percentage)
		Percentage of total	Number per 100 lifts				
June	VI	61.1	1,450	27,622		1,905.6	
July	VI	49.8	1,698	37,710		2,220.8	
August	VI	31.7	1,453	40,050		2,756.8	
June–August				105,382	1,532	6,883.2	—
June	VII	31.3	774	7,995		1,033.4	
July	VII	20.5	567	14,820		2,616.0	
August	VII	13.4	449	12,929		2,878.4	
June–August				35,744	549	6,528.0	36
June	VIII	15.7	277	4,105		1,484.8	
July	VIII	11.3	165	5,773		3,500.8	
August	VIII	6.7	108	3,512		3,248.0	
June–August				13,390	163	8,233.6	34
June	IX	15.5	118	2,420		2,044.8	
July	IX	25.1	87	3,642		4,187.2	
August	IX	19.6	49	2,246		4,603.2	
June–August				8,308	77	10,835.2	47

percent per year. If changes in movements of the fish result in increased availability, the movements do not appear to affect the vulnerable segment of the 1947 year class. The increase in catch per 100 units in

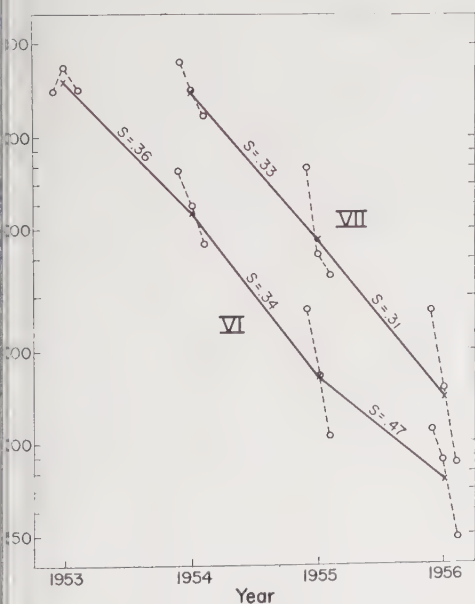


FIGURE 11.—Survival rate of 1947 year-class walleyes calculated for fish 15.1 inches or larger at annulus VI and for those 15.1 inches or larger at annulus VII. Dashed lines represent survival rates month to month in single seasons.

July over June 1953 may be explained by an unusual circumstance that summer. As has already been shown, almost no growth occurred in June of 1953. The condition of the fish in June was also very poor, and many fish up to 16.0 inches long were culled out of the regular catch because they were so thin. After July 15 the condition of the fish improved rapidly. It is therefore probable that many fish of a length that would ordinarily be fully vulnerable to the gear were only partially vulnerable in June and early July because they were thin. When this condition improved in July, these fish were available to the gear. Since fewer lifts were made in July 1953 than in that month of any other year from 1949 to 1956, it might be anticipated that the catch would be higher per 100 lifts in August 1953 than would otherwise be expected. It will be noted that the catch per 100 lifts did not decline from July to August as much as in most seasons. Most of the growth that did occur in 1953 took place in August. Since the portion of the 1947 year class that is over 15.1 inches does not show increased availability to a perceptible degree as the season progresses, the question as to whether growth of the segment of the population shorter than 15.1 inches can account for the change in catch per unit of effort during the season, remains open. Average lengths of commercial fish at the beginning of the growth season, the growth increment during the commercial season, and

TABLE 32.—Decline in the catch of 1947 year-class walleyes larger than 15.1 inches at annulus VII, 1954 through 1956

Month and year	Age group	Fish greater than 15.1 inches		Total number of fish caught	Catch per 100 lifts	Number of lifts	Annual survival (percent)
		Percentage of total	Number per 100 lifts				
1954							
June	VII	69.6	1,721	17,791		1,033.6	
July	VII	52.3	1,441	37,708		2,616.0	
August	VII	36.1	1,209	34,792		2,878.4	
June–August				90,291	1,383	6,528.0	
1955							
June	VIII	46.4	817	12,137		1,484.8	
July	VIII	28.2	410	14,370		3,500.8	
August	VIII	22.3	358	11,616		3,248.0	
June–August				38,123	463	8,233.6	
1956							
June	IX	35.3	270	5,527		2,044.8	
July	IX	43.0	149	6,231		4,187.2	
August	IX	34.8	86	3,977		4,603.2	
June–August				15,735	145	10,835.2	

the percentage of the commercial fish less than 15.1 inches long at capture (Table 28), should throw light on the question.

In 1952, 87 percent of the 1947 year-class fish were below 15.1 inches at capture in June. The average increment by August⁶ of the 1947 fish was 1.12 inches, which resulted in a decrease in the percentage of fish less than 15.1 inches to 66 percent. When the selectivity of the nets is considered, a rapid rise in the catch per unit of effort during the season is to be expected. In 1953, 1954, and 1955, the percentage of fish less than 15.1 inches increased during the season, and the growth increments were considerably smaller than in 1952. The catch per unit effort might be expected to decline under these conditions, but it did not. Fish of the year class as a whole were larger in the later years, and it is presumed that fish shorter than 15.1 inches were closer to full vulnerability than they were in 1952 and therefore needed less increment in length to reach full availability than they did in 1952. Many fish attained a size just below full vulnerability in 1953. It therefore seems probable that growth of incompletely available fish accounted for the increase in catch per unit in these years.

In all years from 1950 through 1955 the catch per unit is higher in the last month of fishing than in June of the following year (Table 29). This observation would seem to indicate a seasonal change in availability (or

high natural mortality), but considerable must be given to two facts before a conclusion is made. The average catch per unit effort any month should be considered as the catch per unit of effort at the midpoint of effort during the month. In June the first few days of fishing usually result in a high catch per unit effort which then declines rapidly during the remainder of the month. The average catch per unit at the beginning of fishing in June is therefore considerably lower than the catch per unit at the beginning of fishing in July. An allowance must also be made for mortality from sources other than regular commercial fishing. During the approximately 9 months of closed season there are several known sources of mortality. First, natural mortality may be substantial, especially during the spawning period. Second, there is gill-netting by the Indians for home consumption and some unreported commercial sales. Third, there is a significant catch by anglers in Upper Red Lake which is made principally from May 15 to June 15 while the fish are still not well dispersed from the spawning streams. These sources of mortality may account for much of the difference between the late summer catch per unit and the catch per unit in June of the following season. Little mention has been made of the density factor of walleyes, but in all years it is lower in June than in the previous August, a factor which also tends to lower the availability to the nets in June. Consideration of all available data strongly suggests that growth during the fishing season is the principal factor bringing about increased availability as the season progresses.

⁶ An increase in size from 13.9 to 15.1 inches would increase the catch per unit slightly more than twofold due to the catch characteristics of the nets.

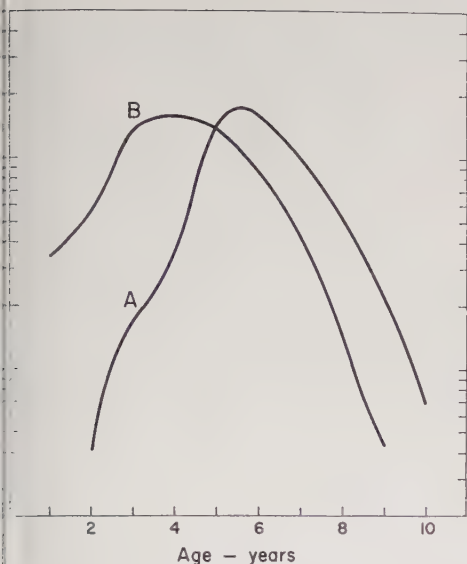


FIGURE 12.—Catch curve of average catch of walleyes: (A) in commercial nets, 1939–1955 year classes; (B) in experimental nets, 1940–1956 year classes. Numbers adjusted to catch per 100 units of commercial gear and equivalent effort with experimental gear.

total mortality of Red Lakes walleyes

To determine the total mortality rate of walleyes a catch curve of the grand average catch per 100 lifts of each age group for the 1949–1957 period was plotted (Table 21, Figure 12A). The right limb of the curve is convex, and apparent mortality ranges from 0.36 between ages VI and VII to 0.66 between ages IX and X. A convex curve indicates declining effort through the period, increasing vulnerability of the fish to the gear with increasing age, higher natural mortality with increasing age, or continual but decreasing recruitment in the age range concerned. In view of the declining recruitment, as shown by the 1947 year class, the last factor is known to affect the shape of the curve. The apparent survival rate of 0.34 between ages IX and X is nearly identical to the rate that applied to the fully vulnerable segment of the 1947 year class (Tables 31 and 32, Figure 11).

Separate catch curves of the 1943–1949 year classes (Table 20, Figure 13) show much variation in both shape and slope and are not entirely consistent with predictions from known mortality rates. The 1945 year class grew faster than later classes and was subjected to even greater fishing effort, but its catch curve has the steepest slope. The possibility of either sampling

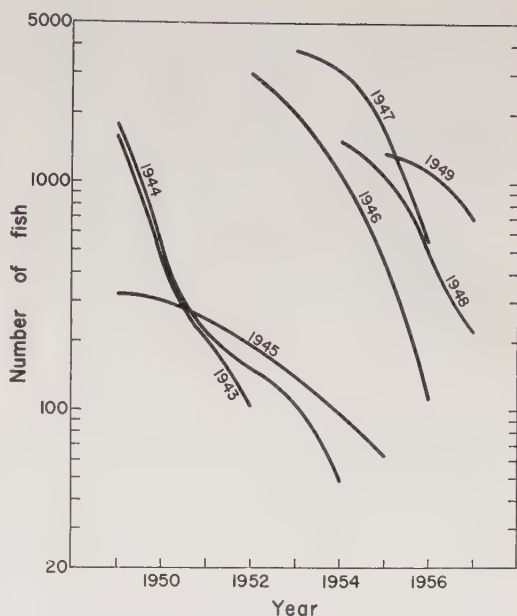


FIGURE 13.—Catch curves of walleyes of individual year classes, 1943 to 1949, in commercial catches of 1949–1957. (Only fish above 15.1 inches included.)

error or mistakes in age determination must be recognized, especially in a weak year class such as 1945. The 1946–1949 year classes all show the effect of recruitment on the curves and all are convex before the eighth year.

A catch curve of the total catch per 30 experimental nets for the 1949–1957 period (Table 18, Figure 12B) is very similar in shape to that derived from the commercial nets of a single mesh size, except that the peak of the curve occurs at age IV instead of age VI and is much more rounded. At corresponding ages the slope of the curve is greater for experimental nets. From age VI to age VII, apparent mortality is 0.51 in contrast to 0.36 from the commercial nets, and from age VIII to age IX it is 0.70 in contrast to 0.66. Experimental nets catch walleyes in the size groups not completely vulnerable to the commercial nets more nearly in proportion to their true abundance in the population than the commercial nets do. This curve must therefore be considered more representative of the true age structure and hence the survival rate than that derived from the commercial net catches.

In this situation the term “mortality rate” is not truly applicable. The catch curve is merely a description of the age structure taken by the nets and may be a rather poor de-

scription of the age structure in the population. It is impossible to evaluate exactly the relative strength of any age group below the size of full vulnerability to the commercial gear. The experimental net catch is more representative of the population structure, but the convex catch curve may also be a reflection of continued recruitment even to these smaller mesh nets. The actual average total mortality rate is probably higher than that indicated by the commercial gear and may be higher than that indicated by the experimental gear.

IMPLICATIONS FOR MANAGEMENT

Certain implications about the use of the fishery statistics for management purposes are made apparent by the changes in catch per unit effort during the season, regardless of their cause. The Red Lakes fishery starts operation on about June 15 and continues until a predetermined quota is filled in August or September. In the present analysis, relative abundance has been determined by the season's average catch per unit of effort. The amount of effort, however, in the various months has varied considerably and affects the season's average catch per unit accordingly. In years when considerable fishing is done in June and little in August, such as 1952, the abundance index for the season will be lower than it would have been if the usual fishing pattern had been followed. In years such as 1954 when little fishing is done in June but much in August and September, the abundance index will be higher. The abundance index is therefore an index of the fish available to the nets for a particular seasonal distribution of effort and may be considerably different for a different distribution of effort. A possible refinement might be the use of the average catch per unit effort for some fixed period (such as July 15 to August 15) as a base for an abundance index, but lack of correspondence between "calendar time" and "biological time" in some years might eliminate any advantages over the present index.

Estimates of year-class strength likewise can be made with a reasonable degree of reliability only by considering the catch rate of a year class over a period of several years in order to balance changes in intensity of fishing from month to month and to take account of changes in growth rate. Such an estimate might be in error because there was variation in mortality from causes other than commercial fishing. If non-fishing mortality is sub-

stantial, ending a season early will result in the loss of many fully vulnerable fish before the next season's fishing takes advantage of their growth increment.

Prediction of future catches would be desirable in most fisheries. Attempts were made to predict abundance of Red Lakes fish, but were as much as 25 percent in error in some years. At the present time no means of predicting growth is known, and several uncontrollable factors, including market conditions, determine the seasonal pattern of fishing. Fluctuations in growth rate have a considerable effect on the time the fish enter the fishery. Variations in the seasonal pattern of fishing can have a profound effect on the apparent abundance of fish. As an example, in 1954 effort was higher than average in June and lower than average in August. By reversing the amount of effort in the 2 months, it can be calculated roughly that instead of approximately 575,000 fish, 710,000 could have been taken with the same amount of effort, giving an abundance index of about 125.0 instead of 101.5. If no fishing had been done in June and the additional effort been expended in August, approximately 830,000 fish could have been taken with the same amount of effort, giving an abundance index of about 145. In this wise, the abundance index in 1954 was higher than it was in 1953. It would appear that the increase was due primarily to the September fishing in 1954, and not due to a greater abundance of fish. Prediction of the next year's catch on the case of a quota fishery, the relative abundance, is not possible with enough reliability to be useful under such circumstances, except for extreme fluctuations in abundance.

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Status of Management of Natural Lakes¹

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ABSTRACT

Lakes of various regions of continental United States and Canada are characterized. Northeastern and Rocky Mountain lakes are predominantly useful for trout and allied species, while those of other areas are managed for a wide variety of species. Major management problems are discussed and current management practices for different fish populations are outlined. Population and habitat control are major management tools. Fish planting has limited use but is effective when properly applied. Major research needs for management include study of fish toxicants, methods of population control, fish planting techniques, and methods of evaluating natural hatches.

INTRODUCTION

There is a large diversity of lake types in the United States and Canada, each of which has problems peculiar to the region, the exploited species, and management techniques available. An effort has been made by the authors of the following discussion to characterize the lakes of the various continental regions, outline their management needs, and summarize the approaches currently being made to fulfill these needs. While any such summary must be quite general, broad trends can be defined which will aid in the understanding of the current status of lake management.

CHARACTERISTICS OF LAKES

Northeastern region

The large numbers of lakes in northeastern states and provinces, together with great differences in soil type, elevation, and size and type of lake, result in an extremely wide diversity of management problems. The region has many deep lakes of oligotrophic type affording conditions suitable for cold-water species such as lake trout and whitefish, but often having shallow areas where warm-water species predominate. There are also many eutrophic lakes, some of which are highly

productive. At the other extreme, dystrophic lakes in bog and mountain areas vary from low productivity to total unsuitability for fish. While the short growing season in the region (especially at high elevations or far north) favors cold-water species, the seasonally high temperatures generally permit spawning of warm-water fish. Introductions of such species have damaged many natural fish population associations in trout lakes.

Although the region has many wild, forested areas, the lakes are mostly accessible from large centers of population and satisfactory angling waters are heavily utilized. Lake surveys began rather early in this region but information adequate for planning effective management is still needed for many lakes. In view of the number and size of the waters, a low-cost, extensive management is generally the type to be expected.

Southeastern region

Most lakes in the southeastern region are situated in low flat lands and average 3 to 5 feet in depth. They were formed by several methods including receding oceans, changing river systems, earthquakes, and the dissolving of limestone to levels lower than present ground water levels. Fluctuations in water level cause extensive changes in area.

According to the U. S. Fish and Wildlife Service's permanent water inventory survey, this region has an estimated 955,410 acres of water in natural lakes. Of this area, Florida has 751,300 acres or 78.6 percent, Louisiana

¹ Based on a symposium of management of natural lakes presented to the annual meeting of the Society at Clearwater, Florida. Panel chaired by Edward E. Hueske.

710 acres or 11.5 percent, Mississippi 40 acres or about 3 percent, and North Carolina 29,250 acres or about 3 percent. Lakes are shallow and not thermally stratified. Natural productivity varies from 100 pounds of fish per acre in infertile sand lakes to as much as 1,200 pounds per acre in more fertile lakes.

North-central region

In those states north of the Ohio and Mississippi Rivers, glacial history of the land determined the origin and characteristics of the lakes. Lakes vary greatly in size as well as in shape depending upon their location, geological origin, and age. There are probably more than 40,000 lakes in the states in this region with Minnesota claiming about 17,000 lakes over 10 acres in size, Michigan counting 37 on their most reliable maps, and Wisconsin reporting 8,676 lakes over 10 acres. Ohio and Manitoba would each no doubt have a great number of lakes to this total. Productivity, spawning facilities, temperature, and oxygen distribution vary considerably from lake to lake and are found linked to geological origin of the lake.

In Minnesota, fishery workers have attempted to classify lakes into the following types according to their species complexes: (1) centrarchid-roughfish; (2) centrarchid; (3) walleye-centrarchid; (4) hard-water walleye; (5) soft-water walleye; and (6) lake trout. Fisheries surveys attempt to determine the type of lake and from this typing management plans are set.

Rocky Mountain region

Since most natural lakes in the Rocky Mountain region lie above 4,000 feet elevation in mountainous terrain, they are generally cold-water lakes which are best adapted to salmonid species. Lakes vary from small alpine cirque-type lakes (above 9,000 feet) to large, hard-water lakes in the mountain valleys. Formed by a combination of glacial and volcanic activity, the majority of lakes are less than 50 acres in area, oligotrophic, and low in dissolved solids. Plankton and bottom-fauna production is poor due to low temperature and lack of nutrients.

Original sport-fish species consisted of cutthroat trout (*Salmo clarki*) with its many hybrid subspecies, the Dolly Varden trout (*Salvelinus malma*) native to parts of Idaho, Montana, and the grayling (*Thymallus*

arcticus) native to the Missouri drainage headwaters. Stocking of other competing species such as lake, rainbow, brown, and brook trout has changed population structures greatly.

MANAGEMENT PROBLEMS

Northeastern region

The two chief problems to solve in improving management of lakes in the northeastern region appear to be: (1) to acquire and maintain public access where needed, and (2) to create or maintain good fish production. To the fishery worker the complexity of these problems is very great. The high cost of lake frontage, the problem of maintaining access for fishing rather than merely for other boating, and the protection of the fish habitat against various forms of damage are a few of the major questions.

Southeastern region

There are seven major fish-management problems in the southeastern states. They may be outlined as follows:

Proper utilization of all fish species.—Many lakes, particularly in Florida, have a much higher production of fish than required by present sporting interests. Commercial utilization of unharvested numbers of sport species has not been successful because sportsmen have an antipathy for commercial interests. Some relaxation in size and bag-limit restrictions is now commonplace in the Southeast, and as a result the increasing numbers of fishermen have obtained greater harvests of crappie, bluegill, redear, and catfishes.

Access.—The need for access has brought about the incorporation of acquisition for public access into the management programs of four southeastern states.

Population controls.—Although evidence points to the beneficial results of reduction in undesired species to favor better growth and production of more valuable species, methods now in use are largely ineffective.

Vegetation control.—Chemical control of noxious aquatic vegetation is presently practiced by six of the southeastern states. Louisiana and Florida, particularly plagued by the exotic hyacinth, *Eichornia crassipes*, are engaged in control of this plant by use of the herbicide 2,4-D, thus making available to fishermen an opportunity to fish in previously inaccessible areas.

Watershed management.—Detrimental watershed-management practices have caused

silting, interrupted water supplies, reduction in size and depth of lakes, destruction of aquatic organisms, and other major ecological changes. Pollution is considered one of the major abuses by five of the nine southeastern states having natural lakes.

Increased production of small lakes with heavy fishing pressure.—Techniques of fertilization, vegetation control, and fish-population control are currently in use in the Southeast in small ponds and lakes. Feeding, to increase the production of game fish and commercial fish in ponds, is also being tested. Considering the expense of adding fertilizer, control of vegetation resulting from such fertilization, and control of undesired fishes, there are difficult problems to solve at present.

Dissemination of public information.—An uninformed public frequently demands use of management methods without regard to requirements of the lakes, economic feasibility, length of time required, or whether the methods have been properly evaluated prior to their use. Education of sportsmen is therefore an important problem.

North-central region

Many of the problems already discussed are also prevalent in the North-central states. Perhaps here each body of water is such a complex network of interrelated and poorly understood environmental conditions, that many fisheries workers can only treat the symptom where the real cause of the problem is very difficult to detect. With so many waters to manage, it is only possible to spend sufficient time on a few lakes to understand their conditions correctly.

Proper use of expensive hatchery or pond-reared fish depends on undeveloped techniques whereby general failure of certain important natural hatches of sport fish can be promptly detected. Slow growth of many centrarchid species which can propagate well but are influenced by a short growing season, especially in the northern states and provinces, is another problem. Proper protection of natural spawning grounds lying outside of the lake bed is needed in the face of shoreline development. Better utilization of the lake productivity through the catch of non-sport fish is generally felt to be required, and better understanding of the ecological role of these species in the lakes is needed.

Rocky Mountain region

In addition to many problems common to other natural lakes of the continent, lakes in the Rocky Mountain region require close examination of temperatures, fertility, fish pressure, fish-population structure, and extent of natural reproduction before proper use of planted trout can be made. The extent of natural reproduction of trout is extremely variable and the use of fingerling or fry planting to control size of year classes involves many problems. Control of undesirable competitive non-sport species of fish depends on complete reclamation in most cases. Introduction of exotic bait fish, although illegal, still occurs.

The limited potential for trout production in many lakes with extremely low productivity must be recognized in management of such waters. Evaluation of management programs using creel census will depend on improved and more economical sampling techniques. The common problem of too few trained fisheries personnel per acre of water is also prevalent here. Those available are heavily used in public relations work where much of their training is not efficiently utilized.

MANAGEMENT PRACTICES AND RESULTS

Northeastern region

Because lakes are individual in nature, relatively few management practices can be applied routinely. Preventive management is an exception. Even though it may not be possible to apply suitable management measures at present, such lakes should not be damaged by failure to take all necessary precautions. Damage from pollution, improper use of weed-control chemicals or insecticides, introduction or spread of undesirable plants, fish or other organisms, and the spoiling of marshes or tributary habitat require increasing vigilance from fisheries workers.

Regulatory measures require much more flexibility than exists at present if they are to be more effective. Statewide regulations are too crude to regulate the total catch of each body of water in accordance with sustainable yield requirements. Regulations are a highly effective tool only where they are sufficiently flexible to adjust the catch from individual lakes.

Size limits are a partially effective method of regulation and assume reasonably low mortality of under-sized fish (low "hooking mortality"). Although difficult to evaluate

applied on a statewide basis because of variations in growth rate, they are useful on species such as muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), and pickerel (*Esox niger*) which are long-lived and particularly vulnerable to capture. Restrictions on manner of taking and against taking of valuable game species are helpful and are used in the region. Special restrictions on the taking of predatory fish to permit an increase in numbers have been effectively used on a limited scale.

Stocking has been widely used in the Southeast where based on the old application of stocking, it was dangerous because locally undesirable species were introduced in many areas.

In most areas some control is now exercised by stocking in accordance with recommendations of surveys. Because results of stocking of fish in lakes are extremely variable, it is desirable to require evaluation through research until a routine procedure can be established. Currently, stocking in the Southeastern region is of three types: (1) in-stream stocking; (2) maintenance stocking of young fish where no reproduction is expected (trout and salmon lakes); and (3) stocking of catchable-sized fish on a put-and-take basis in small ponds. Other types are used in special instances including the stocking of a species when the spawning reserve is depleted or the stocking of predatory fish for biological control.

Fish-population eradication followed by restocking has been successful in restoring some lakes through elimination of undesirable species. Such projects are often limited by the extent of public rights or agreements with landowners and by the size of waters.

Direct methods for control of undesirable species have generally failed in lakes of the Southeastern region. Removal of carp (*Cyprinus carpio*) by netting and control of yellow perch (*Perca flavescens*) and sunfish eggs have not been demonstrated to be practical. Chemical treatment with rotenone, especially for trout in deep water and other fish in shallow water, has shown some promising results (Mullan and Tompkins, 1959).

Indirect methods of control have been successful to some extent. Commercial fishing removes large numbers of fish and in some cases, as in the eastern end of Lake Ontario, there is excellent smallmouth bass fishing adjacent to an area heavily netted for other species. In this case there are indications that commercial fishing may improve

angling. Another indirect method of partial control is through publicity to interest anglers in taking unused species by new methods of harvest, such as archery.

The most promising method of indirect fish-population control seems to be through an increase in numbers of large predatory fish which exert a constant pressure on undesirable species. The control of fish-population balance is evidently the most effective, yet most generally neglected method of fish management. Keeping levels of desirable species high could be expected to provide better fishing for those species since it would increase recruitment and decrease undesirable fish. Control of fish-population balance is considered the only successful method of fish-population control at present. More emphasis on increasing natural spawning is needed in the northeastern region.

If a plan of sustained-yield management is to be developed individually for lakes, it will be necessary to determine or at least estimate what sustained production levels are attainable. Most current production figures represent short-term catch records without establishment of catch-per-unit-of-effort bases and cannot be used to show whether or not total abundance has decreased or increased during the period reported.

Southeastern region

Studies showing the inadequate harvest of many sport-fish species have led to removal of size and bag-limit restrictions in many of the southeastern states. Such management has resulted in increased harvests of several game species, particularly panfish.

Attempts to control the abundance of certain groups of fish to increase the production of desirable species have been most successful in small lakes with controlled inlets and outlets where new immigration of undesirable species was prevented. Removal of forage species in amounts up to 100 pounds per acre in Florida lakes did not result in better fishing for game-fish species nor did the numbers of forage species appear to be reduced materially. Partial reductions in gizzard shad (*Dorosoma cepedianum*) populations were accomplished by applying formulations containing 5 percent rotenone at concentrations of 0.09 to 0.15 p.p.m. to some lakes. In those instances where large numbers of desired predatory fish existed prior to shad removal, the sportsmen benefited by increased catches of the piscivorous game species. Such im-

provement of fishing is apparently associated with reduction in the forage fish available to the predatory species, as well as establishment of better population balance.

Small lakes (up to 250 acres), when managed as outlined by Swingle (1952) and Byrd (1959), have produced catches by sport fishermen in excess of 170 pounds per acre per year. The costs of fertilization and the control of excess aquatic vegetation and undesirable fishes have been approximately 12 to 18 cents for each pound of game fish caught by fishermen.

North-central region

Current fish-management practices in the north-central states are of five general types: (1) improvement and protection of fish habitat; (2) encouragement of natural reproduction of sport fishes; (3) manipulation of fish populations; (4) promotion of adequate harvest of all species of fish; and (5) proper use of hatchery-produced fish.

Because there is a limited amount of information on habitat requirements of many native species and because extensive alterations might be required on the large lakes which predominate, most physical improvements are limited to a small number of lakes. Artificial shelters have been shown to be effective in concentrating panfish and thereby increasing harvest. At present, the protection of water levels, pollution abatement, and soil erosion control are paramount defensive measures employed in this region. The encouragement of natural reproduction of sport fishes has been demonstrated to be effective in limited areas. Although research is still in progress, it appears that this phase of the life history of more desirable predatory fish is the most critical in establishment of strong year classes.

Population manipulation, by which less desirable sizes and species are removed on the assumption that preferred species will then prosper, has not yet proven successful. Thinning and removal operations already carried out have generally failed to remove a sufficient proportion of the fish to improve substantially the growth rate of those fish which remain. Population removal by the use of toxicants has been quite successful in providing ideal habitat for stream trout or warm-water fish species. Stocking of trout in reclaimed lakes appears more effective than the attempts to restock preferred warm-water species.

Rocky Mountain region

Until about 10 years ago, management practices in the Rocky Mountain region consisted almost entirely of the introduction of salmonids. This planting was intended to introduce trout into barren lakes and to improve the angling in lakes already populated with trout. In most cases several species of trout were stocked, probably with the hope that the species best suited to the lake would survive. The original cutthroat trout and grayling populations could rarely tolerate much competition and predation. As a result, stream populations of grayling were lost through competition and the remaining populations are restricted to a few lakes. Rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and lake trout (*Salvelinus namaycush*) now can be found in most lakes. In several large, deep lakes native cutthroat populations have been replaced by lake trout which are quite difficult to catch and extremely predacious. It is doubtful if the trophy-type fishing produced by lake trout is practical for many lakes.

The rainbow trout, which has been planted extensively, is a desirable species because it utilizes many types of aquatic foods and has excellent angling qualities. Since few lakes have facilities for rainbow spawning, year classes can be controlled by fingerling plantings. Most management of the more fertile lakes, especially after reclamation, has included the planting of rainbow trout.

Introductions of brook trout have usually been successful because this species can utilize a wide range of food and will spawn in high altitude lakes fed only by seepage. Frequent plantings have become overcrowded from heavy plantings or natural reproduction. Their slow growth under the rigorous conditions in these lakes eventually reduces angling interest and the overpopulation problem becomes more acute. Although many methods have been tried to prevent overcrowding of brook trout, none has proven consistently successful. Light plantings (200–300 fry per acre) have resulted in faster growing populations but do not prevent overcrowding when natural reproduction is heavy. Reimold (1958) showed how an overcrowded brook trout population could deplete plankton and bottom food. Although brook trout have not always provided high quality angling, this species has proven to be the most adaptable.

under the severe conditions found in high altitude lakes.

Reclamation of lakes with fish toxicants is increasing, but high costs usually limit it to productive and accessible waters. This management practice results in control of undesirable species for periods up to 10 years. Development of better planting practices for lakes has received much study, but few agencies have arrived at sound methods based on adequate research. Although an effective stocking program should be based on data regarding temperatures, fertility, fishing pressure, fish population, and amount of natural reproduction, most stocking programs must be set up without adequate knowledge of the waters. Evaluation of stocking programs is seldom possible. Total dissolved solids, length of shoreline, and predator populations are used as a basis for a system designed to limit different catches per hour in high altitude British Columbia lakes. The most difficult factor to predict or control is natural reproduction, but this problem has been partially solved by using the rainbow trout. The method of fingerling or fry planting to control growth of year classes has definite advantages over the uncertainties and variations in natural reproduction.

In the Rocky Mountain states large populations of longnose suckers (*Catostomus commersoni*), Utah chubs (*Gila atraria*), and yellow perch (*Perca flavescens*) have limited production in many lakes. Partial control of these species has never proven satisfactory. Complete reclamation appears to be the best solution. Although all states in the area prohibit the use of imported live bait in trout waters, it is doubtful if education or more stringent law enforcement will ever completely prevent introductions of exotic species by fishermen.

cursory lake surveys in which routine collections of physical, chemical, and biological data are made have not given the necessary data for management. This information would be of greater value after more long-term management research has been conducted. A census is essential in evaluation of any management program, but unless improved sampling techniques are developed or greater reliance can be made on voluntary censuses, such census work must be limited to passive programs. There has been good cooperation by fishermen on voluntary censuses on a few fishing areas where results of management were apparent.

RESEARCH NEEDS

Northeastern region

In the northeastern region individualized plans for development of management as well as future research work needed for each body of water have been only partially accomplished for some lakes. Such plans should recommend management such as acquisition of public access, regulation of total catch of species needing restriction, improvement of spawning areas if needed, control of undesirable species of fish where needed, maintenance of favorable fish-population balance, as well as types of research needed to handle unsolved problems.

The greatest needs for research work in these states lie in: (1) development of selective poisoning methods for fish-population control; (2) rapid methods for studying fish populations as a basis for establishment of a sustained-yield plan of management; (3) development of better apparatus and techniques for making biological inventories of lakes; and (4) more application of research to management, particularly where evaluation of the results to the angler is needed.

Southeastern region

One of the first research needs in the southeastern region is the classification of natural lakes on the basis of their physical and chemical properties. Following this classification the effectiveness of known management methods may be evaluated for different lake types.

Major research needs in the southeast include: (1) studies on development of better fish toxicants and methods of application for total, partial, and selective reductions of fish populations; (2) studies of proper initial and supplementary stocking including kinds, numbers, and sizes of fish; (3) experimental introduction of new species of sport and commercial fish—the latter to have high public acceptance and also to occupy the highly productive ecological niches now supporting low value fishes; (4) studies in under-harvested lakes to determine best use of productivity and methods to obtain maximum yield consistent with other uses of the body of water; (5) development of better herbicides having no immediate or residual undesirable effects on desirable fishes or fish habitats; (6) studies to provide basis for utilization of fertility presently consumed by unwanted vegetation for the benefit of the fishery; and (7) sound watershed-management planning to prevent

excess siltation or drainage, interrupted water supply, pollution, and abnormal supply of fertilizing elements.

North-central region

In the north-central region, which has a very large number of lakes of diverse types, individual management of each lake is a tremendous undertaking. At present the best manner of handling the management of each lake is on the basis of lake type which must be determined from inventories of physical, chemical, and biological properties. This is much the same problem discussed in the section dealing with the northeastern and southeastern regions. In common with the other regions the north-central states are in need of more economical and reliable fish toxicants for fish-population control, better methods for determination of maximum allowable rates of harvest, and of periodic checks of population sizes of important species. Also there is a need for teams to apply such research developments as are known to fish management together with proper evaluations of techniques. Other research needs of the north-central region should include development of a better technique to detect failure of natural hatches of important species in time to allow supplementary stocking; and accumulation of more knowledge of life history and ecology of sport-fish species especially for use in direction of habitat-control programs.

At the present pace of research development the fisheries managers should be cautioned regarding the premature use of unproven techniques and direct more effort towards the preservation of natural conditions in these

lakes. Such defensive measures are needed to insure that our future sport fishing will have water in which new management, based on future research, can be conducted.

Rocky Mountain region

In addition to many of the research requirements indicated by the other regions the Rocky Mountain region needs studies of (1) fish-carrying capacities for individual multiple species in mountain lakes as related to basic fertility; (2) increase of lake productivity through introduction of fish-food organisms; (3) better planting procedures in relation to fish populations, catch, and limnology of lakes; (4) basal metabolism of fish under various degrees of overcrowding, pollution, and environmental pressure; (5) control of sterilized fish, if they can be developed, better year-class control and for control of overpopulations; and (6) a consolidated research program on fish-population dynamics including fluctuations in natural fish populations and limnology.

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SHORT PAPERS AND NOTES

An Improved Stream Bottom Fauna Sampler¹

Since the square-foot sampler was introduced by Surber (1937) for sampling the bottom fauna of a stream, little advance has been made in the design of stream-sampling equipment and techniques. This may be due to the compactness and ease of using of the Surber sampler, which is a practical and definite advantage when compared with the necessity of walking relatively long distances in stream investigations. Hess (1951) pointed out some of the disadvantages of the use of the square sampler. They are: (1) the difficulty of setting the sampler into the bottom; (2) the loss of large organisms as they crawl out the front of the sampler; (3) rocks and debris drifting into the sampler; and (4) eroding eddies in the front of the sampler. He described a round sampler which could be "turned into the bottom" and which had a hardware cloth mesh in front. These features eliminate the disadvantages of the square sampler.

During the course of our investigations in Valley Creek, a small, rocky stream in Washington County, Minnesota, the Surber sampler was employed, until it became evident that the disadvantages described by Hess, as well as some others, were so serious that the reliability of the samples was much in doubt. The difficulty in setting the square sampler into the bottom was particularly objectionable, as was the difficulty of holding the sampler in place while sampling. A further potential source of error was the normal downstream drift of bottom organisms which enter the net during sampling. Müller (1954) has described the drift as a phenomenon of significant occurrence in streams, and in Valley Creek the drift of certain organisms, such as *Amarrus limnaeus* and *Baetis vagans*, is of considerable magnitude (Waters, 1961). The square sampler, having only hardware cloth mesh in the front, would not eliminate the organisms introduced by drift. Furthermore, it was foreseen that the type of collecting net as used on his sampler would probably make



FIGURE 1.—Sampler being emptied at stream side.

emptying of the sampler difficult, particularly under winter conditions.

A sampler was designed for the Valley Creek investigations which incorporated the advantages of Hess's sampler and also overcame the two principal disadvantages. A circular frame of 13.56-inch diameter (1 square foot in area) was constructed of $\frac{1}{4}$ -inch-diameter metal rod, and a strip of 2-inch-wide sheet metal was attached around the bottom of the frame. The frame was covered with Nitex² of mesh size of 471 microns, 39 meshes to the inch, which satisfactorily prevented drifting organisms from entering the sampler, with the collecting net of the same material extending downstream. The problem of removing the sample from the collecting net was facilitated by attaching, by a zipper, a small collecting bag which, with the sample, could be removed from the sampler, similar to the zipper bag employed on a drag-type sampler introduced by Usinger and Needham (1956).

In operation, the sampler may be turned into the bottom, in a manner similar to Hess's, to the depth of the 2-inch sheet metal, and the sample collected in the usual way without the loss of organisms, erosion around the

¹ Paper No. 4526 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

² Trademark of Tobler, Ernst, and Traber, Inc., New York.

front or sides, or the entrance of drift organisms. An additional advantage especially in sub-freezing temperatures is that by using a number of interchangeable zipper bags and temporarily storing each sample, along with its bag, in a collecting jar for transportation to the laboratory, the emptying and rinsing of the bag in the field may be eliminated (Figure 1). The principal disadvantage of this sampler is that it lacks the compactness of the Surber sampler.

This sampler was developed during investigations supported in part by funds provided by National Science Foundation Research Grant No. F9935.

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Effect of Tricaine Methanesulfonate on Oxygen Consumption of Juvenile Sockeye Salmon

The purpose of this study was to determine the feasibility of applying a constant-flow respirometer to the study of fish-behavior problems. The measurement of oxygen consumption of anesthetized and nonanesthetized juvenile sockeye salmon (*Oncorhynchus nerka*) was used as a test. The resulting data yielded information on the effects of tricaine methanesulfonate (M.S. 222—Sandoz), the anesthetic used, as well as demonstrated the effectiveness of the apparatus.

The test fish were separated into two size classes: (1) "large" fish, 160-180 millimeters fork length; and (2) "small" fish, 60-80 millimeters fork length. Seven anesthetized

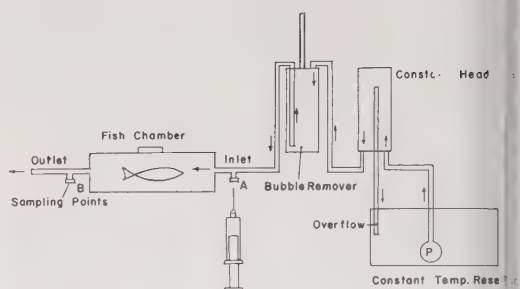


FIGURE 1.—Apparatus used to measure the oxygen consumption of small fish. At each end of the "fish chamber" are rubber diaphragms through which water samples are drawn into a hypodermic syringe (points A and B). The difference in dissolved-oxygen content between inlet and outlet is the amount used by the fish.

large fish and seven not anesthetized were tested individually. The small fish were tested three to six at a time to achieve similar weight groups. Seven groups were anesthetized and seven groups were not anesthetized (Table 1).

The constant flow respirometer (Figure 2)

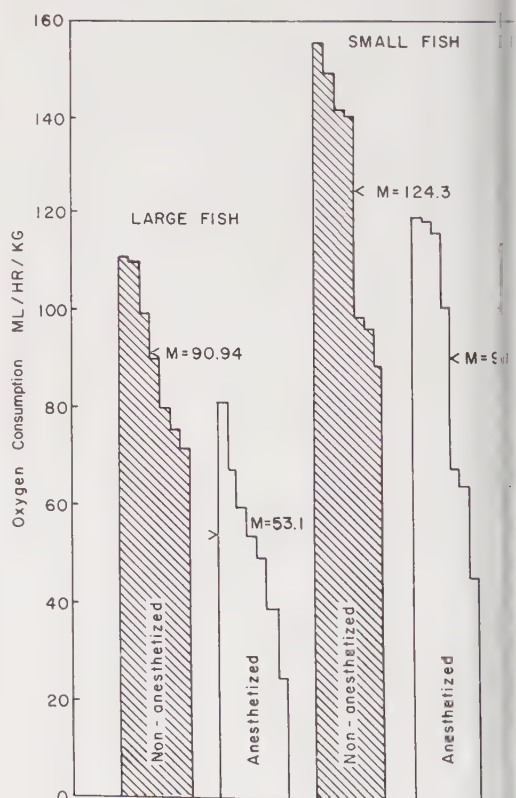


FIGURE 2.—Rate of oxygen consumption for two size classes of sockeye salmon fingerlings.

1.—Oxygen-consumption rates of two size groups of anesthetized and nonanesthetized juvenile sock-salmon

Test number	Large fish ¹			Small fish ²			
	Number of fish	Weight of sample (grams)	Consumption rate (ml/hr/gm)	Test number	Number of fish	Weight of sample (grams)	Consumption rate (ml/hr/gm)
Anesthetized							
	1	34	0.0810	8	6	25	0.1190
	1	46	0.0670	9	6	29	0.1190
	1	26	0.0590	10	6	31	0.1161
	1	58	0.0535	11	4	18	0.1006
	1	60	0.0495	12	6	48	0.0674
	1	28	0.0383	13	6	25	0.0638
	1	48	0.0238	14	4	19	0.0451
Nonanesthetized							
	1	35	0.1113	8	3	17	0.1560
	1	37	0.1105	9	6	53	0.1492
	1	47	0.0995	10	6	44	0.1408
	1	47	0.0895	11	6	53	0.1403
	1	56	0.0795	12	6	50	0.0984
	1	30	0.0748	13	3	29	0.0969
	1	58	0.0715	14	6	57	0.0887

¹—180 millimeters fork length.
²—80 millimeters fork length.

constructed from the description by (1958). The dissolved-oxygen content of the samples was determined by a modified Winkler method. All tests were conducted at a temperature of 14° C. The anesthetic was used at a concentration of 1:20,000. The results not only showed the expected depression of the respiratory rates of the anesthetized fish (Baudin, 1932), but also indicated a uniformity of the drug's effect. It is obvious that the oxygen consumption per unit weight of the small fish is higher than that of the large fish (Figure 2). This difference is apparent not only before but after anesthetization. An analysis of variance indicated no significant difference at the 5 per cent level in the amount of respiratory depression between large and small fish regardless of the rate prior to anesthetization. This indicates that within this species the drug acts uniformly on fish of different sizes.

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Extension of the Range of Northern Pike (*Esox lucius*)¹

Recent technical publications and popular literature have not fully established the present geographical range of the northern pike. A survey by the writer² in 1955 showed that 26 states and Canadian provinces had resident northern pike populations. During the past 5 years pike have been introduced into several other states, thus extending the range. Pike are already established in most of the northern states and are now being released into waters of the south and west.

North Carolina, according to Cornell,³ has attempted to introduce this species in waters of the coastal plains, Piedmont, and mountain sections of the state. These plantings to date appear to be unsuccessful. To our knowledge these releases are the most southern introductions attempted. Maryland has achieved some success in its pike introductions, according to Elser.⁴ Adults and eggs have been planted in the 3,900-acre Deep Creek Lake located in

¹ A contribution of Federal Aid to Fisheries, F-4-R, Job No. 6.

² McCarragher, D. B. (1955) The status of the northern pike, *Esox lucius*, in North America. Paper presented at the 17th Midwest Wildlife Conference.

³ Personal communication from J. H. Cornell, Fish Division, North Carolina Wildlife Resources Commission, January 6, 1960.

⁴ Personal communication from Harold J. Elser, Maryland Department of Research and Education, December 23, 1959.

western Maryland. Pike growth and survival has been recorded, but natural reproduction has yet to be established. Fisheries workers throughout the Mid-south are watching closely the pike releases in Deep Creek Lake in order to evaluate angling and predatory value in Mid-southern waters.

The western range of northern pike in the United States is now extended to Colorado and Montana. Montana has achieved some success with pike introductions in large ranch ponds and small reservoirs throughout the eastern third of the state. Colorado has introduced pike in Bonny Reservoir, Yuma County, and in Skaguay Reservoir in Teller County. These impoundments range in elevation from 3,500 feet (Bonny) to over 10,000 feet (Skaguay). Lynch⁵ indicates that future plantings may be restricted to the eastern section of Colorado, especially the plains area.

The distribution of pike throughout the Canadian Arctic appears sporadic. Conclusive evidence is lacking in some arctic watersheds and more investigational work is needed to determine the exact range status. Hunter⁶ presented a synoptic review of pike distribution in the Canadian Arctic. He mentions that the species is found in some of the coastal streams west of the Mackenzie River to the Alaskan border, where range extension in the Beaufort Sea is possible. It is abundant throughout the Mackenzie watershed including Great Bear and Great Slave Lakes. Pike have been reported from all the rivers emptying into the west coast of Hudson's Bay, south of the Maguse River system. Pike have not been collected from any of the arctic islands.

From the increased interest by fisheries workers throughout the country in the northern pike we can expect to see a continued geographical enlargement of the principal range of the species.

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Natural Mortality of American Shad¹

Since 1950 the Bureau of Commercial Fisheries has studied the American shad (*Alosa sapidissima*) of the Connecticut River to obtain information whereby the population may be managed to obtain optimum sustainable yields. A necessary part of these investigations is the determination of the natural mortality of adult fish.

Few studies have been conducted to determine natural mortality of shad. Fredin (1954) compared the estimated abundance of 6- to 7-year-old fish collected in the Connecticut River in 1946 and 1947, and estimated that the extraneous mortality rate (deaths occurring between fishing seasons) was 10 percent. Talbot and Sykes (1953) reported that adult shad native to streams south of Cape Hatteras, North Carolina, die after spawning. The natural mortality of these fish after initial spawning is presumed to be 10 percent.

In the Connecticut River over 80 percent of the fluctuations in size of runs can be attributed to changes in the size of the escapement from the fishery (Fredin, 1954). Therefore, the number of progeny is dependent on the size of the spawning stock. Using catch and effort statistics supplied by the Connecticut State Board of Fisheries and Game, Fredin presented a method whereby total effort in standard fishing units, fishing mortality rate, and population size could be determined annually. These data are available for each year from 1935 to 1959.²

In addition to the Connecticut River fishery, shad native to this stream are captured along their ocean migration routes from North Carolina to Maine (Talbot and Sykes, 1958). It was estimated by Nichols (1951) that approximately 13 percent of the 1951 shad catch taken by the New York-New Jersey ocean pound-net fishery (16,000 fish) was native to the Connecticut River. It was further pointed out by Nichols that each year during the summer and fall, large numbers of ocean-migrant shad are taken incidentally by the Gulf of Maine by purse seiners.

¹ Part of the shad investigation being conducted by the Bureau of Commercial Fisheries to furnish information to the Atlantic States Marine Fisheries Commission.

² 1935-51, Fredin (1954); 1952-59, unpublished data, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina.

⁵ Personal communication from Tom M. Lynch, Colorado Game and Fish Department, December 24, 1959.

⁶ Personal communication from J. G. Hunter, Arctic Unit, Fisheries Research Board of Canada, March 16, 1960.

TABLE 1.—Number of shad in each age group caught per 100 standard units of fishing effort, Connecticut River

	Age group						
	III	IV	V	VI	VII	VIII	IX
	25	2,202	1,698	1,913	283	25	0
	114	975	5,448	1,485	545	193	18
	19	1,714	2,775	3,983	720	419	78
	18	1,039	4,417	2,728	816	223	46
Age							
number	44	1,482	3,584	2,527	591	215	36
Natural log							
of average							
number	3.784	7.301	8.184	7.835	6.382	5.371	3.584

causes of mortality of adult shad native to Connecticut River, exclusive of that from fishing within the river, are: (1) natural causes during or following spawning within the river; (2) natural causes at sea; and (3) fishing outside of the river. These mortalities were grouped and termed natural mortality. The natural mortality rate plus the fishing mortality rate is equivalent to total mortality rate (Ricker, 1958). Since natural estimates of the fishing mortality rate are available, the natural mortality rate can be determined if the total mortality rate is known.

MATERIALS

Shad scales were collected in the Connecticut River throughout the 1956–59 fishing seasons (April 1 to June 15 of each year) to obtain samples which were representative of the catch. From 1956 through 1959, 720, 582, and 616 shad were sampled in the respective years. Length, weight, and sex were determined, and plastic impressions of scales from each fish were read by two biologists using an Eberbach projector. Less than 1 percent of the scales were discarded as unreadable. Total age and number of times spawned were determined for all fish. Annuli and spawning marks as age indicators of shad have been validated.³

MORTALITY DETERMINATIONS

Total mortality estimates were obtained from both age- and spawning-group frequencies during the period 1956–59. A number of assumptions underlie this method of mortality estimation. According to Rounsefell and Everhart (1953) they are: (1) annual recruitment to the population was constant at

TABLE 2.—Number of shad in each spawning group caught per 100 standard units of fishing effort, Connecticut River

Year	Spawning marks					
	0	1	2	3	4	5
1956	3,610	1,849	639	146	34	0
1957	5,413	2,221	891	217	111	0
1958	4,200	3,250	1,671	610	153	42
1959	4,337	3,271	1,297	338	100	39
Average						
number	4,390	2,648	1,124	328	100	20
Natural log						
of average						
number	8.387	7.909	7.025	5.793	4.605	2.996

¹ Spawning group denotes number of spawning marks.

the time each age group entered the fishery; (2) ages can be deciphered with a high degree of accuracy; (3) natural mortality has been constant over the period involved; (4) fishing mortality has been uniform over the period involved; (5) mortality rate of fully vulnerable age groups is equal between age groups; and (6) age samples are representative of the vulnerable age groups. These assumptions appear reasonably satisfied in this study, but as pointed out by Ricker (1958) rarely are all the theoretical requirements fulfilled.

The catch by age and spawning group for each year adjusted to 100 standard fishing units of effort was determined (Tables 1 and 2). Because there were fluctuations in year-class strength, the age- and spawning-group distributions for the 4 years were combined to obtain an estimate of average abundance. Beverton and Holt (1956) state that average abundance can be used to obtain an approximation of total mortality if the assumption is made that natural mortality is fairly constant over the period under consideration.

Shad native to the Connecticut River spawn for the first time at 3, 4, or 5 years of age. Since age-group VI is the first age group in which practically no maiden fish occur and in which all fish are fully vulnerable to capture, only frequencies of age-groups VI through IX were used to determine total mortality rate (Table 1). Some shad spawning for the first or second time (0 or 1 spawning mark on scales) are not large enough to be fully vulnerable to capture by the commercial fishery. Only fish with two or more spawning marks, therefore, were used to determine total mortality from spawning-group frequencies (Table 2).

Total mortality rates were calculated from the average age- and spawning-group distributions by a method of Rounsefell and

study, Mayo H. (Manuscript) Validity of age determination from scales of marked American shad. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina.

Everhart (1953). The estimated total instantaneous mortality rate was 1.35 using age-group frequencies and 1.27 using spawning-group frequencies, or an average of 1.31. The instantaneous rate was converted to an annual rate of 73 percent (Ricker, 1958). If the average annual fishing mortality rate is known for the period under consideration, then the average annual natural mortality rate can be determined from Ricker's (1958) formula:

$$a = m + n - mn$$

where a is the annual total mortality rate, m is the annual fishing mortality rate, and n is the annual natural mortality rate. From unpublished data⁴ it was calculated that the average annual fishing mortality rate on shad fully vulnerable to capture (fish larger than 16.7 inches fork length) over the period 1956-59 was 36 percent (range 30-40 percent).⁵ The estimated average annual natural mortality rate during the period 1956-59 was therefore 58 percent.

The high natural mortality rate of adult shad is verified by the scarcity of older age groups in the catch and the preponderance of newly matured fish. This phenomenon has been found not only for the Connecticut River population but also for all Atlantic coast populations south to Chesapeake Bay.

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⁵ Includes both sport and commercially caught fish.

Variations on Rereading Walleye Scales¹

Ricker in his *Handbook of Computation for Biological Statistics of Fish Populations* (1958, page 185) points out that although the scale method has proved to be of general applicability in determining the age and growth of fishes, "no one claims that all age determinations are infallibly accurate and the older fish present considerable difficulty." The following observations may help in evaluating the validity of scale reading and may give more perspective in evaluating data derived from such studies.

From December 1936 to June 1944 most of the author's research involved scale reading and analysis of data thus secured. Since 1946, scale-reading experience has largely been in teaching students and in checking their results. Recently, however, I had occasion to examine scales from 671 walleyes, *Stizostedion vitreum*, from Clear Lake, Iowa (Carlander and Whitney, 1961). While I have studied scales of many species of fish, my most extensive growth studies have been on walleyes. Their scales can present more than average difficulty in interpretation. The scales of one population may be more easily read than those of another, and those from the Clear Lake population are easier than average.

To avoid possible biases, scales were always read without knowledge of the size of the fish. Since in this particular study determination of the abundance of various year classes was an important consideration, the scale envelopes collected from 1954 through 1958 were mixed so that the date of collection was as not known at time of scale examination. The scales were read from plastic impressions at the positions of the focus, the various annuli, and the anterior margin of the scale were marked on strips of stiff paper for use on a nomograph (Carlander and Smith, 1941). Impressions were made of three to four scales from each fish and usually all impressions were examined before one was read. Scales of about 45 fish were read per hour. The entire series was read a second time, after

¹ Journal Paper No. J-3921 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project 1374, Iowa Cooperative Fisheries Research Unit sponsored by the Iowa State Conservation Commission and Iowa State University of Science and Technology, with the cooperation of the Fish and Wildlife Service, United States Department of Interior, and the Sport Fishing Institute.

1.—Number of Clear Lake walleyes in each group as finally assigned (A), number for which the first two readings did not agree (B), number in which even two out of three readings failed to agree (C)

[Percentages are given in parentheses]

A	B	C
6	—	—
31	4 (13)	—
132	21 (16)	—
174	25 (14)	2 (1)
121	47 (39)	16 (13)
107	54 (50)	11 (10)
50	33 (66)	8 (16)
33	20 (60)	8 (24)
9	4 (44)	2 (22)
5	—	—
1	1 (100)	1 (100)
2	1 (50)	1 (50)
671	210 (31)	49 (7)

ing so that the scales would not be in same order. The ages secured in the two readings did not agree for 31 percent of the (Table 1). In most of the cases (80 percent) the ages were within a year of each other but for three fish the ages were years apart and one fish was listed as age and VII.

The fish for which the first readings did not agree were read a third time, after mixing again without knowledge of size of the fish or year of collection. Of 210 fish, the third reading did not agree with either of the first in 49 cases. A fourth reading resulted in ages matching for each of the fish, except which with a fifth reading was successfully assigned to age-groups IV, V, VIII, and VI.

The problem seems to be one of failure to recognize annuli. Failure to get agreement on the first two readings occurred even in older fish, although the percentage increased with age. The criteria used in identifying the annuli were: (1) crowding of the annuli; (2) a wide space between series

of circuli particularly at the antero-lateral angle; and (3) anastomosis of circuli particularly on the lateral fields. The third criterion was considered most significant. Study of the scales failed to reveal any criteria which did not involve some subjectivity. Anastomosis of one or two circuli did not usually mean the presence of an annulus.

It was noted that the scales of the 1952 year-class fish were much clearer at ages II and III than were those of the 1954 year class. The 1954 year class showed somewhat faster growth averaging 7.3, 12.4, 15.3, and 17.0 inches at the first through the fourth annulus in comparison to 7.5, 11.4, 14.6, and 16.5 inches for the 1952 year class (Carlander and Whitney, 1961).

Despite the nonrepeatability of some of the scale readings, the data derived on the basis of the final readings indicate that the readings are probably accurate (Carlander and Whitney, 1961). Ages of individual fish cannot be assessed with a great deal of certainty, but the errors will average out or will be submerged to the degree that bias does not interfere with general interpretations when samples are large. The degree of nonrepeatability of readings, of course, will differ with populations, species, and biologists.

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REVIEWS

EDUCATION AND RECRUITMENT OF OCEANOGRAPHERS IN THE UNITED STATES. *A report by the Committee on Education and Recruitment, American Society of Limnology and Oceanography, Inc., August 30, 1960. Limnology and Oceanography, Supplement to Volume VI. 1960. 23 pp., 2 figs., 4 tables.*

The American Society of Limnology and Oceanography and The Committee on Education and Recruitment deserve credit for recognizing and accepting their responsibility in the education and recruitment of marine scientists. The Committee reports on employment and production of oceanographers, and discusses opportunities and needs in the basic disciplines—biological, chemical, geological, and physical oceanography. The report is well written and organized and contains information of interest to all persons engaged in aquatic sciences. Copies may be obtained from Dr. George H. Lauff, Secretary-Treasurer, American Society of Limnology and Oceanography, University of Michigan, Ann Arbor, Michigan.

The mechanics of such a survey usually present many problems concerning the coverage of institutions for interview and the manipulation of resultant data. That these problems confronted the Committee is evidenced in footnote 3, page viii.

The statistics reported in this and the following sections of the present report are neither complete nor exact. This is because of the varied nature of the institutions engaged in oceanographic work, the lack of agreement on the definitions of the various categories involved, and the different interpretations which may have been applied to the question by those who answered the questionnaires. . . . Nevertheless, the Committee believes that the numerical information presented supplies a useful indication of the manpower engaged in oceanography. . . .

I hesitate to criticize this report adversely, because (1) it includes much information of value to marine scientists, (2) of my sincere respect for the Committee members who are leaders of note in their respective fields, and (3) as a member of ASLO, I take pride in the Society's publications. To rationalize my position, I consider the subject matter of such import that the limitations and questioned areas of the report cannot be ignored.

The area of disagreement concerns data in Section III—Employment, and the use and conclusions reached from these data in subsequent sections. A major objection is the interpretation of data published in 1959 by the National Academy of Sciences—National Research Council, *Oceanography 1960 to 1970. Chapter 12—Marine Sciences in the United States—1958*. This NAS article listed 70 marine laboratories and summarized results of a survey from 60 of these, but gave no implication that personnel at the 60 institutions represented the total oceanographic working force of scientists in the United States. The ASLO article, on the other hand, accepted NAS figures for the 60 laboratories as the total working force, after apparently deducting approximately 350 visiting scientists from the NAS total of 1,548. ASLO then applied a percentage increase to the NAS figure and concluded that the 24 institutions selected for its survey represented nine-tenths of the present working force. I cannot

agree that these institutions include such a percentage or that they are representative of distribution of the oceanographic disciplines. Marine institutions were not considered, industrial laboratories were not even mentioned, and only two fishery agencies, Alaska and Virginia, were included in the list. There are more than 20 coastal states and at least 10 of these maintain a sizable staff of marine scientists. Biological oceanographers (ASLO definition) predominate in these fishery laboratories, and, if included in the survey, could substantially change the percentage representation of the several oceanographic disciplines in the total working force. Support of this statement can be found in Cader's paper, *A Survey of Technical Fishery Personnel* (Transactions of the American Fisheries Society, Volume 88, pages 18–22, January 1959). His data show over 1,600 technical fishery personnel in the United States, a third of which are in marine fisheries. Using the 15 percent mean annual rate of increase listed by ASLO, the number employed in marine fisheries alone during 1960 would exceed 629 in the ASLO list in all biological oceanography.

The seriousness of this omission, in terms of percentage representation by discipline, is difficult to determine, but personal knowledge of several industrial laboratories and many of the state agencies omitted leads me to question the ASLO figures. Further, use of these figures to point out that the work force of physical oceanographers is greater than the production does not seem justified. None of the following undocumented statement warranted it suggests a preconceived notion as to the output of the ASLO survey. “. . . The need for strengthening this field [physical oceanography] is confirmed by the fact that there is at present a greater demand for physical oceanographers for employment than for men trained in any of the other specialties.”

It would appear from ASLO's own figures (persons employed and mean annual rate of increase) that the demand for physical oceanographers is greater than the demand in some of the other disciplines.

During this period of expansion—perhaps the most important to the field of oceanography—a urgent front is a necessity, and any discourse favoring one oceanographic discipline above another only impede the progress of marine science.

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ECOLOGY OF INLAND WATERS AND ESTUARIES.
George K. Reid. Reinhold Publishing Corp., New York. 1961. 375 pp., 112 figs., 14 tables. \$5.00.

Here is a textbook which presents a concise yet comprehensive introduction to the present state of knowledge of the geological, physical, chemical, and biological processes operating in inland and estuarine waters. With the rapidly developing integration of estuarine ecology from marine ecology (oceanography), Dr. Reid's contribution is timely and particularly noteworthy in presenting comparisons between fresh, inland, and estuarine water

st, comparisons between estuarine and marine have been the rule, with emphasis on the marine spectrum of the estuary at the expense of fresh-water spectrum.

Organization of the book is in five parts: Part I, Origin and Features of Basins and Channels, a chapter on lakes, streams, and estuaries, respectively; Part II, The Nature of Water (one chapter); Part III, Natural Waters as Environment, having a chapter each on light, temperatures, movements, dissolved gases, and dissolved solids; Part IV, Organisms in the Environment, including a chapter on protists and plants, and one on animals in aquatic environments; and Part V, Relationships of Organisms and Environment, with chapters on aquatic populations and a chapter on communities.

Parts I and III follow the classic scheme of presentation used in most texts on limnology, differing only by the addition of discussions concerning lakes and estuaries. Of the approximate 185 pages of the two parts, about 45 pages concern streams (including a discussion of channel forms and characteristics), and 30 pages pertain directly to estuaries. Usually, many of the basic principles, discussed in relation to lakes, apply directly to streams and estuaries, thus accounting for the disproportion in presentation. Unfortunately, separating the discussions of various environmental factors for three types of aquatic systems causes repetition and confusion which might have been avoided. However, a careful re-reading should quickly eliminate the slight confusion.

The second and fourth parts are straightforward. The last two chapters on populations and communities in the aquatic environment represent the bulk of the book in the title. In these chapters Dr. Reid discusses the principles of population and community ecology in an integrated approach. The concepts of aquatic community appear, to this reviewer, to be well covered by the approach of W. C. Allee, to whom the chapters, in part, are dedicated. Most of the terms and concepts presented in this section can be found in standard aquatic publications.

The bibliography of 16 pages represents most of the important publications in the aquatic sciences published in many recently published works. Unfortunately, the post-war works on estuaries in Australia, Africa, and Asia have not been cited. The chapters of Part IV each have a short bibliography.

The book is noticeably free of typographical errors. The error on page 159, line 7, "... 0.0000001 of hydrogen ions. . . ." should be "... 0.0000001 of hydrogen ions. . . ."), attractively bound, and at a convenient size. It should prove a useful addition to the libraries of aquatic biologists.

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WATER FISHES IN MISSISSIPPI. By Fannye A. Reid. Mississippi Game and Fish Commission, Jackson, Miss. 1959. 239 pp., 40 figs., 4 tables, \$3.00.

This review in Copeia, 1960, No. 4, by Milton B. Manly, gives the details of arrangement of sub-chapters, and so this review will be devoted to pointing out errors and omissions.

In the Preface, Dr. Karl F. Lagler is credited with identifying a number of specimens of *Hybopsis*. This apparently is an error in acknowledgment and Dr. Ernest A. Lachner should be the person thanked. The latter is given some acknowledgment on page 128.

There are a number of typographical errors, e.g., page 43, line 16, "eggs hatch in larval forms"; p. 55, l. 18, *L. platostemus* should read *L. platostomus*; p. 57, l. 38, *chaseii*, other places this specific name is *chaseii* which is the way Wailes spelled it; p. 91, last line of key, *Opsopoeodus* should be *Opsopoeodius*; p. 170, couplet 5 of key *Lepomis cynellus* should be *Lepomis cyanellus*; p. 211, l. 22, "both lakes and streams"; etc. These are some of the errors that were noticed by a hurried scanning of the publication. The misspelled technical names are the more serious mistakes, but fortunately there are only a few.

On page 43 the author says, "suctorial mouth without functional jaws." This could be interpreted as meaning lampreys have jaws but that they are nonfunctional; I suggest deletion of the word, functional.

The author states in the general discussion of lampreys on page 43 that the ammocoetes live in the mud of quiet backwaters. I disagree because ammocoetes almost invariably live in silt pockets or bars behind (downstream from) logs and rocks in the channel or along the margins of the channel downstream from bank projections, debris, logs, etc. The "pockets" of silt are a result of eddy currents, and presumably the same currents bring food material within reach of the filter-feeding ammocoetes.

Unfortunately the section on garfishes was not edited carefully. There are numerous errors and perpetuations of fishermen's yarns. The key on page 54 gives the lateral line scale count of 59 to 64 for *Lepisosteus platostomus* which is correct, but then on page 58, the 14 specimens (thought to be *L. platostomus*) from the Pearl River have a scale count ranging from 53-56, and on page 63 in Table I, the three specimens of shortnose gar have 53, 55, and 56 lateral line scales. Obviously the latter counts (14 specimens from the Pearl River and the three referred to in Table I) are those of the spotted gar. Actually there are no authenticated records of *L. platostomus* from the Pearl River, and my collecting during the past 12 years has not revealed any.

The name *Lepisosteus oculatus* Winchell, 1864, should be used instead of *L. productus* Cope, 1865. I have not had the opportunity to hunt for Wailes' specimen of *L. chaseii*. Apparently the mounted specimen was part of a private collection which probably no longer exists. The published description is inadequate for species determination, and so unless the specimen is found, the name *L. chaseii* cannot be recognized nor can it be correctly referred to the synonymy of any particular species. Of course, if the specimen is found and is a spotted gar, then the name *L. chaseii* could replace *L. oculatus*.

The longnose gar, *Lepisosteus osseus*, is an inhabitant of rivers as well as of lakes. They usually occur in the current in the main channel, and I would debate that they prefer quiet water.

Spotted gar 7 or 8 feet in length and a weight of over 300 pounds (page 57) is preposterous. Is the author speaking for herself when she says, "It is believed . . ." (p. 57, l. 6)? Then too, whom is the author referring to on p. 57, l. 24, when she says, "It is claimed by some that the shortnose gar, *L. platostomus*, reaches a maximum length of only 2 to 3 ft." Also in the same paragraph, reference to an

8-foot specimen is a guess based on a photograph. This nonsense should have been left out of an otherwise rather technical publication.

There are other errors in the descriptions of the different species of garfishes, especially of the younger stages. Some of these mistakes are the result of misidentifications, others probably because of lack of sufficient material to determine entire range of variation.

On page 97, last line, the statement is made that habits and environmental preference appear to be the same for both *Hybognathus nuchalis* and *hayi*. Published information (Kemp and Hubbs, Texas Jour. Sci., 1954, 6(1):113) and my own observations show that although the two species occasionally occur together they usually occupy different habitats.

There are numerous distribution records that can be added. For example, *Notropis camurus* occurs in the upper Pearl River system; *Hiodon tergisus* occurs in the Pearl River; *Hybopsis aestivalis* is a common form in the Pearl River and lives in the Mobile Bay drainage, Escambia River, and the Choctawhatchee River systems to the east; and *Heterandria formosa* is common around Pearlinton, Mississippi, and west into Louisiana to New Orleans and even westward beyond Raceland, Louisiana, on the west side of the Mississippi River. However, I agree that it is probably an introduced species into these areas. *Ammocrypta asprella* is a common species in the Pearl River; *Moxostoma carinatum* occurs in the Pearl River and drainages to the east (Robins and Raney, Copeia, 1957 (2): 154); *Notropis roseus* should be *Notropis texanus* (Suttkus, Copeia, 1958 (4):307-318); and *Etheostoma histrio* is a common species in the Pearl River and occurs eastward to the Escambia River.

Considering the limited amount of material that was examined, the *Freshwater Fishes in Mississippi* is a fine compilation and should be useful to the layman as well as the student. Unfortunately, the author did not attempt to examine any of the vast number of Mississippi specimens in the Tulane University fish collection.

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TROUT FARMING. By David B. Greenberg. Chilton Company, Philadelphia. 1960. 197 pp., 158 figs. \$12.00.

Private fish farming in the United States, including the raising of trout for commercial use, is growing at a steady rate. For this reason there is need for a book which would deal with the business of raising trout. Mr. Greenberg's book has just this aim. The best chapters deal with construction and operation of hatcheries; water supply; construction and use of incubators, tanks, and ponds; sorting and grading of fish; and transportation equipment. One of the most complete chapters is on the incubation of trout eggs. The whole book is excellently illustrated, and the author must be congratulated on the abundance and quality of the photographs which he collected from world-wide sources. Unfortunately, some of the photographs, for example Figure 80, are accompanied by incorrect legends.

Other chapters which deal with trout biology,

anatomy, physiology, and nutrition are too sketchy and do not measure up to the rest of the book. In the chapter on trout nutrition, commercial dry feeds are discussed almost exclusively. This is unfortunate because research on trout nutrition has not advanced far enough to permit production of stable dry diets giving uniformly satisfactory results with all salmonid fishes under divergent conditions. While in some cases dry pellets seem to be excellent, serious nutritional disorders are common in other instances.

The chapter on trout diseases received an undox treatment, since the discussion was limited solely to reproduction of fish disease leaflets from the Eastern Fish Disease Laboratory of the U. S. Fish and Wildlife Service. These leaflets were not considered by their respective authors as comprehensive sources of information and are intended to be used as an introduction to the annotated references attached to each leaflet. The value of leaflets with the references included is much reduced.

The bibliography lists references in five languages in addition to those in English. More American and Canadian references would enhance the value of the book.

Undoubtedly, this book should be of great practical value to trout hatchery men but cannot be considered as a complete and a well-balanced manual of trout farming.

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STYLE MANUAL FOR BIOLOGICAL JOURNALS. By the Conference of Biological Editors, Committee on Form and Style. American Institute of Biological Sciences, Washington, D. C. 1960. 92 pp. \$3.00.

The recently published *Style Manual for Biological Journals* is the result of several years' work by the committee of the Conference of Biological Editors. It was designed to assist the research worker to prepare manuscripts for publication in biological journals and for use in the instruction of students. The book consists of eight sections, the first two of which comprise the greater part of the volume and are designed specifically for the author. The remaining sections are primarily for the editor and referee but also contain suggestions for handling papers which will be found useful by the scientific writer. Section I is essentially a condensed set of directions for expository writing. It includes many suggestions concerning proper diction and the concise presentation of material without unnecessary wordage. Although it is very helpful, it cannot and certainly was not intended to be a substitute for adequate training in expository writing. The advocacy of use of the pronoun "I" in exposition is felt to be most unfortunate since such usage concentrates the reader's attention on the writer rather than on the work, and in cases where the author was helped by others can lead to cumbersome references and possible absurdities. A particularly useful portion of this section encompasses lists of approved abbreviations, compound words, expression of numerical systems, geographic and geological names, and numerals. One caution expressed by the committee which this reviewer feels should have received greater emphasis is that while abbreviations are

, they should be employed sparingly through-
out text, and further that approval of a list of
variations is not to be construed as license for
indiscriminate use.

The section on preparation of copy is especially
valuable for authors and if followed closely will mini-
mize the nagging mechanical errors of form which
bother all editors. Individual editors and journals
prefer some forms not recommended, but these
variations will be minor. More comprehensive treat-
ment of methods for preparation of art work and
illustrations would have been desirable, but it is presumed
that the necessity for brevity precluded more detailed
treatment and discussions.

This manual is not as comprehensive as the U. S.
Government Printing Office *Style Manual*, and the
reading editor must consult this latter work or some
other equally inclusive work for details not covered
in this manual for biological journals. Authors, how-
ever, will find the more condensed treatment easier
to use, and it is to be hoped will in consequence
use it freely. Significant omissions in the list of
recommended references are the new work by Tre-
visan and a revision of Fowler especially designed
for American usage.

While individual editors will take exception to
many recommended usages and a second edition
undoubtedly will contain changes where the usages
proved objectionable or cumbersome, this man-
ual represents a great step forward in the tremendous
task of preparing material for publication. It may
yet pave the way for consolidation of editorial
standards which will facilitate biological publication in
face of continually expanding production and
rising printing costs. The manual can be highly
recommended to all prospective authors.

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IN MEMORIAM

Brian C. Curtis, St. Helena, California

G. P. Halferty, Seattle, Washington

Richard I. Stevens, Rome, New York



Donald S. Rawson

1905-1961

Donald S. Rawson, a limnobiologist of international fame and head of the department of biology, University of Saskatchewan, died suddenly on February 16 following a heart attack. He was born in 1905 at Claremont, Ontario, and took his undergraduate and graduate training at the University of Toronto, specializing in limnobiology. In 1928 he joined the staff of the department of biology, University of Saskatchewan at Saskatoon, Saskatchewan. In 1949 he became head of the department.

Dr. Rawson's studies in limnology extended over a period of nearly three and a half decades and were carried out on the large lakes of western Canada and the Northwest Territories. The work involved physico-chemical, biological, and fisheries studies and specific experiments in fisheries management. He is especially known for his work on Reindeer, Athabasca, and Great Slave Lakes. Through his studies and some sixty stimulating publications, the North Canadian lakes have become as familiar to fresh-water biologists

all over the world as any of the "classic" lakes of limnology. Although all his studies were carried on in Canada, in outlook he was international. He traveled widely in the United States and in Europe and became thoroughly familiar with leading limnological investigations abroad. In addition to his achievements in research he made substantial contributions as a teacher in his chosen field, and his students occupy important scientific posts in many parts of the world.

Many honors came to Dr. Rawson in his lifetime. He was president of the Limnological Society of America, president of the Canadian Conservation Association, director of the Fisheries Research Board of Canada, a member of the Royal Commission on Fisheries for Saskatchewan, and a fellow of the Royal Society of Canada. His work on the editorial board and several committees of the American Fisheries Society contributed in many ways to the Society's development. At the time of his death he was at the very peak of his scientific and teaching career.

